RALPH N. HINTON

# CALIFORNIA FISH and GAME

"CONSERVATION THROUGH EDUCATION"

VOLUME 82 WINTER 1996 NUMBER 1

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# CALIFORNIA FISH AND GAME

VOLUME 82 WINTER 1996 NUMBER 1

*Published Quarterly by*

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Emerald Bay, Lake Tahoe ..... ..... Photograph by R. Dunham, date unknown

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*California Fish and Game* 82(1):1-41 1996

# OBSERVATIONS ON THE MACROBENTHOS OF LAKE TAHOE, CALIFORNIA-NEVADA

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**Lake Tahoe is a large, deep, oligotrophic lake supporting a diverse and abundant macrobenthos. Since 1904, occasional collections of benthos have been made and results reported. This paper describes the most intensive study, which was carried out in 1962 and 1963 by the California Department of Fish and Game and the Nevada Division of Wildlife. Three hundred and ninety-one Ekman grab samples were collected from widely scattered locations. The benthic invertebrate community was dominated numerically by oligochaetes, amphipods, ostracods, and dipteran larvae, in that order. The variety of benthic invertebrates decreased with depth. Oligochaetes, amphipods, and turbellarians were abundant in the deepest waters. The estimated standing crop was 2500 invertebrates/m² with a wet weight of 6 g/m². The depth distribution of gastropods, plecopterans, and pelecypods was correlated with deep-water plant beds. Benthic invertebrates were most numerous at the two shallowest depth zones at South Lake Tahoe and McKinney Bay. Ten invertebrates are endemic to Lake Tahoe: one free-living ostracod, two amphipods, two free-living turbellarians, two plecopterans, and three oligochaetes. Further studies of the Lake Tahoe macrobenthos are recommended since the existence of some species may be threatened by water quality changes associated with cultural eutrophication.**

## INTRODUCTION

Lake Tahoe has an unusual assemblage of benthic invertebrates, but little information has been published on this subject. The bottom flora is also unusual, but little is known about it. Frantz and Cordone (1967) briefly described the deep-water plant beds of Lake Tahoe, but more needs to be learned about Tahoe's benthic community. We are publishing this largely historical description of the macrobenthos to inform those who make decisions regarding urbanization in the Tahoe Basin that the lake supports an unusual and complex benthic community, including some species apparently not found elsewhere. This community is fragile and sensitive to

[1] Mr. Frantz is deceased. This publication is dedicated to his memory.

[2] Mr. Cordone is retired from the California Department of Fish and Game.

changes induced by humans (Frantz and Cordone 1967, Richards et al. 1991). If Lake Tahoe's rare beauty and endemic life forms are to survive, changes that reduce the superb clarity of the lake and impacts of introduction of exotic organisms must be avoided.

## STUDY AREA

Lake Tahoe is a cold, extremely oligotrophic lake located at an elevation of 1,899 m in the Sierra Nevada of California and Nevada (Fig. 1). It averages 313 m deep, has a maximum depth of 501 m, and a surface area of 499 $km^2$ (see also McGauhey et al.[3] 1963). Bottom sediments are described by Court et al. (1972).

## HISTORY OF STUDIES

### Studies Before 1960

Limnological studies, prompted by increased concern about the welfare of Lake Tahoe, began around 1960. Before 1960, despite Tahoe's special position among the world's lakes, very few studies or even simple identifications of its invertebrates were made.

The first study was cited by Ward (1904:137): "Some collections of Entomatraca [sic], made in the lakes of the Sierras, by G. Eisen, were studied by Lilljeborg and reported by de Guerne and Richard (1889). The localities are given in general terms, except for *Epischura nevadensis*, which was collected in Lake Tahoe and Echo Lake . . ." The second study was made in the summer of 1904 by Juday (1907). From plankton hauls, he identified rotifers, copepods, and cladocerans. In the summer of 1913, Kemmerer et al. (1923) conducted a limnological study of Lake Tahoe which included observations on the zooplankton. Pilsbry (1934) listed a gastropod from Lake Bigler, the old name for Lake Tahoe. Hanna and Smith (1937) described mollusks collected from deep water in the summers of 1933 and 1936. Their records were supplemented by van der Schalie and Berry (1948), who identified mollusks taken from a shallow, rocky shoal. Finally, a gastropod (Baker 1911:211) and a freshwater sponge (de Laubenfels 1932:110-111) from Lake Tahoe were reported.

### Studies After 1960

The Lake Tahoe Area Council, with funds provided by the Max C. Fleischmann Foundation of Nevada, sponsored a comprehensive study of Lake Tahoe in the early 1960s (McGauhey et al.[3] 1963). However, bottom sampling was limited and only 15 samples were collected with an orange peel grab in July 1962.

Goldman (1974) described the benthic invertebrates from 41 bottom samples evenly distributed over Lake Tahoe in grid fashion. Sampling was conducted

[3] McGauhey, P.H., R. Eliassen, G. Rohlich, H.F. Ludwig, and E.A. Pearson. 1963. Comprehensive study on protection of water resources of Lake Tahoe Basin through controlled waste disposal. Prepared for Lake Tahoe Area Council, Engineering Science, Inc., Oakland, California, USA.

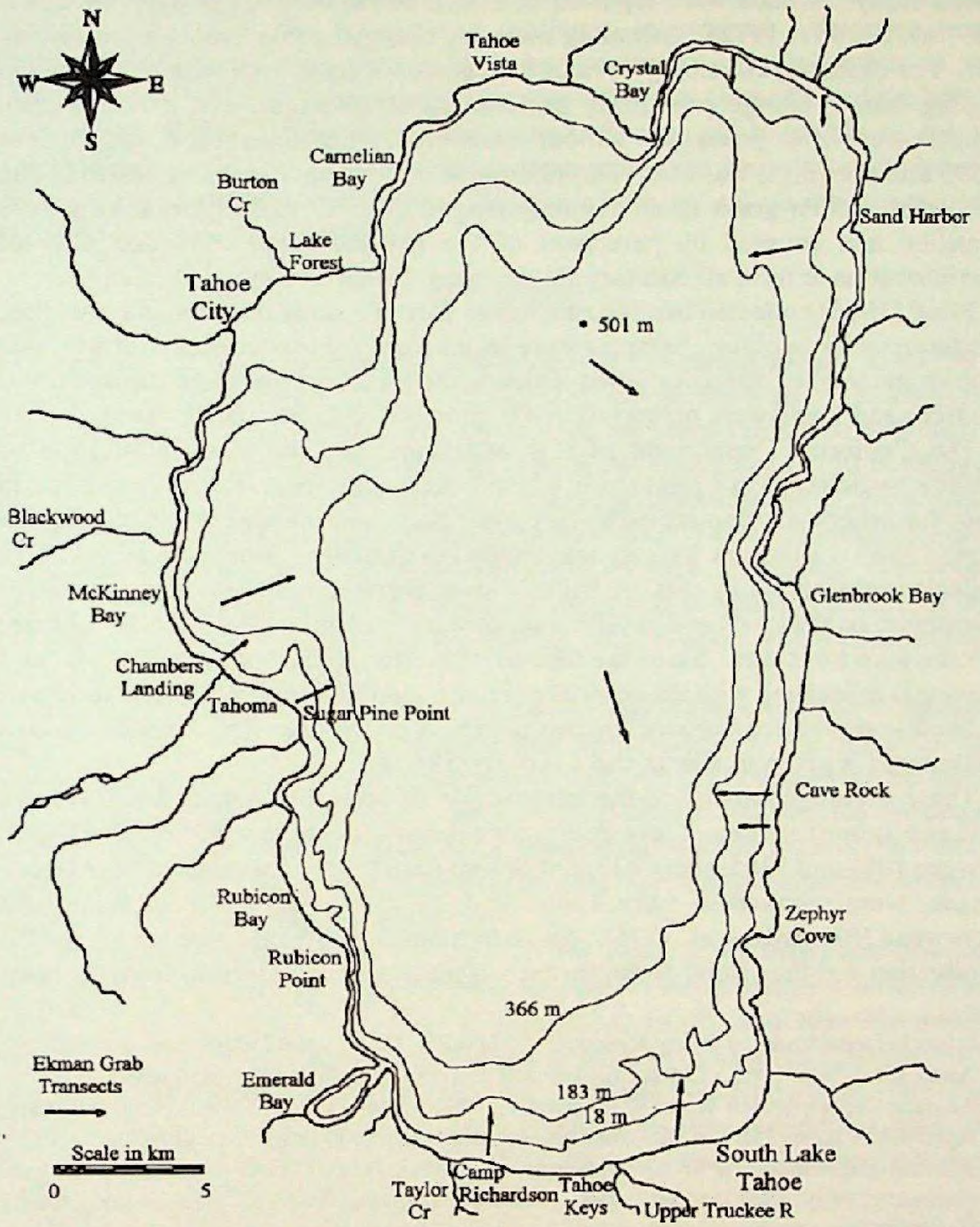


Figure 1. Map of Lake Tahoe showing important localities and Ekman grab transects.

between 1 August and 26 October 1968 using a Shipek sampler. The material was sieved through a screen fine enough to retain cladocerans and copepods, but sieve size was not specified.

Bottom invertebrates were sampled during the California-Nevada-Federal (CNF) Joint Water Quality Investigation of Lake Tahoe, a cooperative effort supported by state, federal, and local public agencies. The benthic work was a minor aspect of the

overall study. Results were reported in annual summaries (CDWR[4] 1966, 1967, 1969, 1970, 1971, 1972). Sampling methods changed considerably from year to year. For example, collecting devices included an Ekman grab with an automatic tripping frame, orange peel grab, artificial substrate cages, and a Ponar grab. Samples were often processed without screening. When screened, a No. 30 sieve (0.595 mm openings) was used. Sampling in the littoral zone was emphasized. The number of bottom grabs taken annually ranged from 19 to 59. Organisms were identified and counted by personnel of the Federal Water Pollution Control Administration at the Taft Sanitary Engineering Center in Cincinnati, Ohio.

Flint[5] (1975) collected benthic samples as part of a study on the signal crayfish, *Pacifastacus leniusculus*. Samples were taken along three transects with a Shipek sampler and washed through a series of sieves, the smallest with 60-$\mu$ mesh openings. The flora and fauna were preserved in 4% formalin and identified to genus.

The California Department of Fish and Game and the Nevada Division of Wildlife participated in a joint study of the Lake Tahoe sport fishery from 1960 to 1966; the fishery was dominated by lake trout, *Salvelinus namaycush* (Cordone and Frantz 1966). Lake trout biology was studied to determine if new organisms were needed to supplement its diet. A benthic invertebrate survey provided qualitative information on the kinds and relative abundance of potential food items to compare with the lake trout diet. Since the lake trout is strongly bottom oriented, its food likewise is associated with the substrate (Frantz and Cordone 1970). The results of the benthic survey are described in this paper. A preliminary check list of the taxa encountered is given in Frantz and Cordone (1966).

These investigations led to the introduction of opossum shrimp, *Mysis relicta*, into Lake Tahoe to augment lake trout forage (Linn and Frantz 1965, Hanson 1966). Between 1963 and 1965, about 333,000 shrimp from Upper Waterton Lake, Alberta, Canada, were released in Lake Tahoe and, by 1971, they were abundant and widespread (Richards et al. 1975). An unfortunate and unanticipated result of this introduction was the virtual disappearance of planktonic cladocerans from the main

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[4] California Department of Water Resources (CDWR). 1966. Lake Tahoe, annual summary, April 1965-June 1966. California-Nevada Joint Water Quality Investigation.
California Department of Water Resources (CDWR). 1967. Lake Tahoe, annual summary, April 1966-April 1967. California-Nevada Joint Water Quality Investigation.
California Department of Water Resources (CDWR). 1969. Lake Tahoe, third annual summary, May 1967-March 1968. California-Nevada-Federal Joint Water Quality Investigation.
California Department of Water Resources (CDWR). 1970. Lake Tahoe, fourth annual summary, July 1968-June 1969. California-Nevada-Federal Joint Water Quality Investigation.
California Department of Water Resources (CDWR). 1971. Lake Tahoe, fifth annual summary, July 1969-June 1970. California-Nevada-Federal Joint Water Quality Investigation.
California Department of Water Resources (CDWR). 1972. Lake Tahoe, sixth annual summary, July 1970-June 1971. California-Nevada-Federal Joint Water Quality Investigation.

[5] Flint, R.W. 1975. The natural history, ecology, and production of the crayfish, *Pacifastacus leniusculus*, in a subalpine lacustrine environment. Ph.D. Dissertation, University of California, Davis, California, USA.

body of the lake. Richards et al. (1975, 1991) and Morgan et al. (1978) attributed the loss to predation by *M. relicta* and, perhaps, introduced kokanee salmon, *Oncorhynchus nerka*. The shrimp likely had an impact on the benthos as well (Richards et al. 1991). Cultural eutrophication also may have affected the bottom community (Goldman 1988). Because these changes are relatively recent, the bottom fauna information described in this paper represents the most comprehensive baseline to compare against the dual impacts of the *M. relicta* introduction and accelerated cultural eutrophication.

## METHODS

A standard 15.2-cm Ekman grab was used to sample from about 1 m to 150 m. A hand-operated winch was used to deploy and retrieve the grab. Frequently, the grab was lowered several times before a satisfactory sample could be collected. A modified 22.9-cm Ekman grab sampled depths exceeding about 150 m (Rawson 1947). The modifications included a wide flange surrounding the 22.9-cm grab to promote horizontal stability and two treadles attached to the flange which closed the jaws automatically, but only when both treadles were depressed. To combat problems associated with excessive drift, sampling was confined to periods of calm weather. The system worked well in the flat, silt substrate which dominates the deepest waters of Lake Tahoe.

Collection sites were located along transects roughly representative of the north, east, south, and west quadrants and the lake center (Fig. 1). In 1962, 124 grab samples were taken from seven depth zones, and in 1963, 267 samples were collected from nine depth zones (Table 1). The three deepest zones in 1962 and the two deepest in 1963 were on the lake-center transects. Various factors, particularly the weather, prevented sampling all depth zones in all seasons. Occasional shoreline collecting by hand supplemented the grab samples.

Grab samples were transferred to containers, labeled, and taken to a laboratory for immediate processing. Bottom material was strained through a series of four Tyler Standard Screens (U.S. series equivalent 14, 18, 25, and 30). The smallest sieve (No. 30, 0.595 mm openings) retained organisms as small as cladocerans and copepods. However, various studies (e.g., Nalepa and Robertson 1981) have demonstrated that this sieve size does not retain smaller individuals of several groups, particularly turbellarians, nematodes, oligochaetes, cladocerans, ostracods, copepods, and chironomids.

The organisms and remaining detritus were placed in a white enamel pan with a saturated Epsom salt solution that relaxed and floated most specimens. All organisms visible to the naked eye (macrobenthos) were removed with forceps or pipettes and preserved in 99% isopropyl alcohol or 10% formalin. Most organisms were alive when removed from the substrate material. Invertebrates were separated by major taxonomic groups, counted, and weighed, when feasible. Some were measured and amphipod eggs were counted. Representatives of a particular species or group were wet-weighed to the nearest 0.01 g. Finally, representative specimens from various depths and locations were sent to authorities for identification.

Table 1. Lake Tahoe benthic invertebrate sampling schedule, 1962-63.

| | 1962 | | 1963 | |
|---|---|---|---|---|
| Depth zones (m)* | Number of samples | Months sampled | Number of samples | Months sampled |
| 1-2 | 0 | | 33 | Jul, Aug, Oct, Dec |
| 5-10 | 31 | May, Jul, Aug, Oct, Dec | 48 | Feb, Apr, May, Jun, Jul, Aug, Oct, Dec |
| 15-30 | 29 | May, Jul, Aug, Oct, Dec | 48 | Feb, Apr, May, Jun, Jul, Aug, Oct, Dec |
| 30-50 | 0 | | 12 | Aug, Oct, Dec |
| 60-90 | 32 | May, Jul, Aug, Oct, Dec | 48 | Feb, May, Jun, Jul, Aug, Oct, Dec |
| 100-110 | 0 | | 11 | Aug, Oct, Dec |
| 120-150 | 23 | Jul, Aug, Oct, Dec | 48 | Feb, May, Jun, Jul, Aug, Oct, Dec |
| 180-250 | 4 | Aug, Sep | 0 | |
| 225-300 | 0 | | 9 | Feb, Aug, Oct, Dec |
| 350-400 | 2 | Aug, Sep | 0 | |
| 450-500 | 3 | Dec | 10 | Feb, Aug, Oct, Dec |
| Total | 124 | | 267 | |

* The depth zones were originally organized using the English system. Conversion to the metric system accounts for the awkward values.

Because of improved collecting procedures for the smaller organisms, the 1963 data are more representative than the 1962 data of the true depth distribution and relative abundance of the Lake Tahoe benthos. These refinements account for the greater number of major invertebrate groups identified in the 1963 samples. In 1962, cladocerans and copepods were combined, nematodes were mistakenly lumped with the oligochaetes, and the two families of dipteran larvae (Chironomidae and Ceratopogonidae) were not separated.

# RESULTS

## Depth Distribution and Relative Abundance by Major Taxonomic Category

The variety of benthic invertebrates in Lake Tahoe decreased as depth increased. At <30 m, all 12 major taxonomic groups identified in 1962 and all 17 identified in 1963 were represented. Between 30 and 150 m, all 12 taxa again were represented in the 1962 samples and 16 out of 17 in the 1963 samples. At >150 m, six out of 12 and 10 out of 17 taxa were represented.

The benthic invertebrate community of Lake Tahoe is dominated numerically by oligochaetes, amphipods, ostracods, and dipteran larvae, in that order (Appendices 1, 2, 3, and 4). Numerically, oligochaetes exceeded all other groups in all depth zones, except for amphipods in several of the deeper ones. Oligochaetes represented between 26 and 62% of invertebrates sampled in all but one depth zone. They were abundant in coarse sand in shallow water, sand and silt substrates at intermediate depths, and silt in the deepest waters. Mean densities commonly exceeded 1,000 worms/$m^2$.

Amphipods were the second most abundant group. Two genera were collected: *Stygobromus* and *Hyalella*. The highest concentrations were recorded from >100 m where mean densities >500/$m^2$ were common. *Stygobromus* was absent from depths <30 m and *Hyalella* was not recorded at depths >30 m. Between 21 and 44% of the grab samples taken at depths <30 m contained *Hyalella*. *Stygobromus* was present in 8-46% of the samples between 30 and 90 m and in virtually all samples taken at greater depths.

Other relatively abundant and widespread invertebrate groups were ostracods, turbellarians, and dipteran larvae. Maximum mean ostracod densities were recorded at intermediate depths, with a peak in 1962 of 484/$m^2$ in the 60-90 m range and 1266/$m^2$ in this same range in 1963. Ostracods occurred in >75% of the 1963 samples and made up about 10-30% of the total mean number of organisms taken at all but the shallowest and deepest depths. The lowest counts (<25/$m^2$) were recorded from >450 m.

Although variable in abundance, turbellarians were common at all depths. Maximum mean densities in 1962 were recorded at >450 m (370/$m^2$) and at 60-90 m (124/$m^2$). Highest values in 1963 occurred at >30 m (about 100-350/$m^2$). At these depths, flatworms made up about 5-10% of the total invertebrates. The fewest specimens were taken from the shallowest depths sampled (1-2 m). The frequency of turbellarians in the samples increased from about 10 to 50% as depths increased to 30 m and then remained between 50 and 100% from 30 m to the greatest depths.

The density of dipteran larvae was inversely related to depth. In 1962, densities exceeded 300/$m^2$ at depths <30 m, but declined at greater depths; none were collected in three samples taken from >450 m. Chironomids were separated from ceratopogonids in 1963. Most of the latter were taken at <10 m while chironomids were present at all depths. Concentrations exceeded 600/$m^2$ in the 1-2 m zone and decreased to about 30/$m^2$ at >450 m. Chironomid larvae were found in about 70-95%

of the samples at all depths, except those >120 m, where their frequency declined to about 65%.

Stoneflies, mites, snails, and clams were absent or rare at >150 m. Stoneflies were most numerous at 60-90 m (38/m² in 1962 and 80/m² in 1963). Lesser numbers were recorded at 15-30 m and 120-150 m in 1962 and 100-110 m in 1963. They were absent or rare at other depths. Highest frequencies (about 20-40%) occurred between 50 and 150 m.

Mites were found over a wide range of depths, but were not abundant. Densities varied greatly by depth, but were generally highest at <100 m, where they ranged between 22 and 31/m² in 1962 and 27 and 85/m² in 1963. They constituted about 1% of the total number of invertebrates taken at these depths. About one-third of the samples at <100 m contained mites. Few were captured in deeper water. The depth record was a single specimen collected at 232 m in McKinney Bay.

The distribution and relative abundance of gastropods and pelecypods were similar. They were most abundant from 15 to 90 m, where their densities approximated 50/m² and they occurred in about one-third of the samples. Maximum mean snail densities were about 200/m² in the 15-30 m depth range in 1962 and 50/m² in the 60-90-m range in 1963. Highest clam densities were 40/m² in 1962 and 51/m² in 1963, both from 60-90 m. The densities of snails and clams declined progressively in both shallower and deeper water. Few were taken from <15 m or >90 m and none were found in the deepest waters. They seldom constituted >1% of the total invertebrates collected.

Copepods and cladocerans were a major component of both the benthos and the plankton of Lake Tahoe. Copepods were widely distributed and common in substrate samples. They were present in about 30-75% of the grabs. Mean densities ranged between 30 and 72/m² from the shallowest depths to about 110 m. At these depths, copepods represented about 1-4% of the total invertebrates collected. Concentrations declined to about 10/m² in deeper water. A copepod taken at 482 m was the deepest recorded. Cladocerans in the benthos were most dense (about 250/m²) at < 50 m, declining to about 40/m² between 60 and 90 m, and to only 2/m² at >225 m. They made up about 5-15% of the total number of organisms to 50 m and <1% at greater depths. At <110 m, cladocerans occurred in about 35-85% of the samples, and at greater depths they were found in only 10% of the samples. The deepest recorded was a cladoceran taken at 477 m.

Other invertebrates were much less abundant and widespread. Free-living nematodes, for example, never represented >1% of the total mean number of organisms collected at any depth. Means ranged from 3 to 14/m², and none were found in the 1-2-m and 100-110-m zones. Nematodes occurred in about 20% of the samples at >120 m. With two exceptions, hydroids were restricted to between 30 and 110 m and mean densities from 10 to 35/m². About 10-15% of the samples at these depths contained them. Leeches were generally restricted to 5-90 m, and densities of 3-29/m². They occurred in about 5-20% of the samples, where they constituted <1% of the total organisms sampled. None were recorded from >100 m or from 1 to 2 m. Trichopterans were seldom encountered. Mean densities were 4/m²

in the 5-10 m depth zone and 2/m² in the 60-90 m zone. Ephemeropterans were recorded only from the two shallowest depth zones. About 24% of the samples at 1-2 m and 6% of those taken between 5 and 10 m contained mayfly nymphs. The mean densities for these depth zones were 31 and 4/m², respectively. However, the true numerical status of mayflies is probably underestimated because little effort, aside from occasional collections by hand, was devoted to sampling the very shallow rubble areas where they would normally be found. For the same reason, the numbers of other aquatic insects may also be underestimated.

Other benthic invertebrate studies of Lake Tahoe have yielded similar results. McGauhey et al.[3] (1963) confirmed the strong dominance of oligochaetes followed by dipteran larvae and amphipods. Goldman's (1974) results were somewhat atypical in that amphipods were the most abundant invertebrate group, representing about 28% of the 892 organisms collected. Oligochaetes (25%) were second and ostracods (17%) were the third most abundant. Flint[5] (1975) recorded oligochaetes, ostracods, and dipterans as the numerically dominant groups. Unique to his study were nematodes, which were abundant and diverse at two of the three transects.

Results of the CNF Study demonstrated that relative abundance changes dramatically with the method of collection (CDWR[4] 1966, 1967, 1969, 1970, 1971). The CNF Study compared bottom grab samples with samples taken from artificial substrate cages (rock-filled wire baskets) suspended 2-3 m off the bottom for 3 months. Although the relative abundance of the major taxonomic groups they collected by grab sampling was very similar to what we found in the 1-2 m depth zone with our Ekman grab, their cage samples yielded more specimens and species of mayfly nymphs and caddisfly larvae and relatively fewer oligochaetes. The major difference, however, rested with dipteran larvae. Artificial substrate cages yielded more species and twice the number of midge larvae as the grab samples. Apparently, rocks in cages provide a firm, nonshifting surface for attachment by the dipterans and very little in the form of sediment for burrowing oligochaetes. Although variability between stations was considerable, midges made up roughly 70% of the invertebrates collected in cages and about 30% of those taken in grab samples. The latter figure is close to the percentage of dipterans at 1-2 m (Appendix 2).

## Standing Crop Estimates

Lakewide mean standing crops (number/m² and g/m²) were derived by weighting estimates of mean density and mean wet weight for each depth zone by the fraction of Lake Tahoe's surface area represented by that depth zone. Only 1963 data were used for this purpose since they were more complete and reliable, and more depth zones were sampled. The standing crop estimates are only approximations. The paucity of samples taken from >150 m is a weakness. Not only is the sample size small, but depths between 150 and 225 m and 300 and 450 m were not sampled in 1963.

The standing crop of Lake Tahoe macrobenthos approximated 2,500 invertebrates/m², with a wet weight of 6 g/m² (60 kg/ha) (Table 2). Of these totals, oligochaetes made up about 40% by number and 65% by weight. They were

Table 2. Standing crop estimates for Lake Tahoe macrobenthos, 1963.

| Depth range (m) | Turbellaria | | Oligochaeta | | Ostracoda | | Amphipoda | | Diptera | | Gastropoda | | Others | | All organisms | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | g/m² | % | g/m² | % | g/m² | % | g/m² | % | g/m² | % | g/m² | % | g/m² | % | g/m² | % |
| 1-2 | 0.007 | 0.5 | 0.510 | 39.2 | 0.027 | 2.1 | 0.008 | 0.6 | 0.275 | 21.2 | 0.195 | 15.0 | 0.278 | 21.4 | 1.30 | 100 |
| 5-10 | 0.048 | 1.3 | 2.396 | 65.6 | 0.048 | 1.3 | 0.120 | 3.3 | 0.216 | 5.9 | 0.586 | 16.1 | 0.236 | 6.5 | 3.65 | 100 |
| 15-30 | 0.060 | 1.1 | 2.562 | 48.3 | 0.083 | 1.6 | 0.031 | 0.6 | 0.450 | 8.5 | 1.804 | 34.0 | 0.310 | 5.8 | 5.30 | 100 |
| 30-50 | 0.215 | 1.8 | 8.032 | 66.1 | 0.254 | 2.1 | 0.003 | 0.0 | 0.116 | 1.0 | 3.228 | 26.5 | 0.312 | 2.6 | 12.16 | 100 |
| 60-90 | 0.195 | 2.0 | 7.858 | 80.1 | 0.380 | 3.9 | 0.350 | 3.6 | 0.332 | 3.4 | 0.434 | 4.4 | 0.261 | 2.7 | 9.81 | 100 |
| 100-110 | 0.400 | 4.7 | 6.584 | 77.6 | 0.125 | 1.5 | 0.901 | 10.6 | 0.149 | 1.8 | 0.240 | 2.8 | 0.091 | 1.1 | 8.49 | 100 |
| 120-150 | 0.120 | 6.3 | 1.036 | 54.5 | 0.073 | 3.8 | 0.504 | 26.5 | 0.114 | 6.0 | - | - | 0.053 | 2.8 | 1.90 | 100 |
| 225-300 | 0.127 | 2.1 | 3.085 | 51.9 | 0.064 | 1.1 | 2.638 | 44.4 | 0.021 | 0.4 | - | - | 0.005 | 0.1 | 5.94 | 100 |
| 450-500 | 0.219 | 3.5 | 4.265 | 68.3 | 0.007 | 0.1 | 1.704 | 27.3 | 0.019 | 0.3 | - | - | 0.026 | 0.4 | 6.24 | 100 |
| Lakewide weighted g/m² | 0.18 | 3.0 | 3.82 | 64.6 | 0.05 | 0.8 | 1.49 | 25.2 | 0.08 | 1.4 | 0.22 | 3.7 | 0.07 | 1.2 | 5.91 | 100 |
| Weighted kg/ha | 1.8 | | 38.2 | | 0.5 | | 14.9 | | 0.8 | | 2.2 | | 0.7 | | 59.1 | |
| Weighted no./m² | 158 | | 994 | | 146 | | 877 | | 112 | | 5 | | 250 | | 2542 | |
| % | 6.2 | | 39.1 | | 5.7 | | 34.5 | | 4.4 | | 0.2 | | 9.8 | | 100 | |

followed by amphipods, which contributed 35% by number and 25% by weight. Remaining groups of invertebrates contributed much less to the total standing crop compared with these two dominant categories. Gastropods made up about 4% of the total mean wet weight, but shell weights were not subtracted to arrive at organic weights.

## Role of Deep-water Plants

Lake Tahoe supports a remarkable zone of deep-water macroscopic plants (Frantz and Cordone 1967), including various species of algae, mosses, and liverworts. Plants taken in Ekman grab samples and bottom trawls during fish collections supported an abundance of invertebrates, especially gastropods, plecopterans, pelecypods, and amphipods. The depth distribution of the first three groups of organisms was roughly correlated with that of the plants. Amphipods, however, attained maximum densities at >150 m where no macroscopic plants were found.

Observations of the contents of the Ekman grab samples permitted a comparison of macroinvertebrate occurrence and density in the presence and absence of plant material. Plants were most abundant at 61-107 m (Frantz and Cordone 1967). Within this zone, macroinvertebrates occurred most frequently in grab samples containing plant material (Table 3). The density and frequency of occurrence of amphipods, plecopterans, gastropods, and pelecypods were substantially higher in samples containing plant fragments. In the 60-90 m range, the density of these organisms in collections containing plants averaged >10 times that of collections without plants.

The importance of deep-water plants to the distribution and density of macroinvertebrates may be underestimated. Invertebrates are probably disturbed by the grab during its descent through the plants and while it rests on the substrate awaiting the messenger. Under these conditions, the more active organisms may move away from the grab and thus avoid capture.

## Distribution by Locality

Bottom samples collected in 1963 permitted a qualitative comparison of macrobenthos at four different locations: Cave Rock, South Lake Tahoe, McKinney Bay, and Crystal Bay (Appendix 5). In general, the six most abundant groups of invertebrates in the two shallowest zones (1-2 m and 5-10 m) were more abundant at South Lake Tahoe and McKinney Bay than at Cave Rock and Crystal Bay. No obvious relationships were noted for the remaining depth zones. Sampling in 1962, although more limited, yielded similar results.

Shallow water grab sampling carried out by the CNF Study (CDWR[4] 1970, 1971) generally agreed with our findings. In 2 different years, maximum densities of organisms were recorded off Tahoe Keys. Relatively high densities were also recorded off Tahoe City, Chambers Landing, and Taylor Creek. Glenbrook Bay, Rubicon Bay, Tahoe Vista, Zephyr Cove, and Crystal Bay yielded fewer invertebrates. Density estimates from rock substrate cages at these localities were much more uniform with no localities clearly dominant over others.

Table 3. Relationship between macrobenthos and deepwater plants as indicated by bottom sampling in Lake Tahoe, 1962 and 1963.

| Depth range (no. samples, % with plants) | Category | Amphipoda | | Plecoptera | | Pelecypoda | | Gastropoda | | All organisms | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | With plants | Without plants | With plants | Without plants | With plants | Without plants | With plants | Without plants | With plants | Without plants |
| 30-50 m (N =12, 42%) | Total organisms | 0 | 1 | 0 | 0 | 5 | 0 | 9 | 2 | 568 | 642 |
| | Mean no./sample | - | 0.1 | - | - | 1.0 | - | 1.8 | 0.3 | 113.6 | 91.7 |
| | Frequency of occurrence | - | 14% | - | - | 40% | - | 40% | 29% | 100% | 100% |
| 60-90 m (N = 80, 66%) | Total organisms | 485 | 32 | 108 | 9 | 82 | 4 | 87 | 1 | 4947 | 1795 |
| | Mean no./sample | 9.2 | 1.2 | 2.0 | 0.3 | 1.5 | 0.1 | 1.6 | 0.0 | 93.3 | 66.5 |
| | Frequency of occurrence | 55% | 11% | 51% | 15% | 42% | 11% | 49% | 4% | 100% | 100% |
| 100-110 m (N = 11, 64%) | Total organisms | 89 | 86 | 5 | 0 | 0 | 1 | 4 | 0 | 488 | 238 |
| | Mean no./sample | 12.7 | 21.5 | 0.7 | - | - | 0.2 | 0.6 | - | 69.7 | 59.5 |
| | Frequency of occurrence | 100% | 100% | 50% | - | - | 25% | 33% | - | 100% | 100% |

## Species Distribution, Taxonomy, and Biological Notes

Ninety-five taxa of Lake Tahoe macrobenthos were identified from specimens collected in the early 1960s (Table 4). Ten of these are new species believed to be endemic to Lake Tahoe. These include two plecopterans, three oligochaetes, one ostracod, two amphipods, and two turbellarians. The species shown in Table 4 are only those identified by specialists for each group. The following descriptions, however, include these species as well as other species reported from Lake Tahoe.

### *Porifera*

Freshwater sponges did not occur in our grab samples. The senior author identified a specimen of *Spongilla* taken by hand in 0.3 m of water east of the mouth of Burton Creek. However, sponges may be relatively common in the littoral zone, according to results of the CNF Study. *Spongilla* was found in artificial substrate cages set off the mouth of Emerald Bay, Tahoe Keys, and Tahoe City (CDWR[4] 1969). An early reference to freshwater sponges in Lake Tahoe appeared in de Laubenfels (1932:110) who identified *Spongilla lacustris* and stated, "These bright green digitate fresh-water sponges were collected by Prof. W.K. Fisher, of Stanford University, at Lake Tahoe, elevation 2,040 meters [sic], August, 1925."

### *Coelenterata*

Twenty-eight of the 29 specimens of *Hydra* sp. collected in 1963, and identified by the senior author, were taken at the south end of the lake between 39 and 104 m. One specimen was taken in 1.2 m in McKinney Bay. Scant mention was made of coelenterates in other studies of the benthos of Lake Tahoe; however, McGauhey et al.[3] (1963) collected the freshwater jellyfish, *Craspedacusta sowerbyi*, at 4 m in Glenbrook Bay.

### *Turbellaria*

Free-living, freshwater planarians are common in Lake Tahoe. Two endemic species are present. One is very widespread, ranging from shallow water to the greatest depths, and the other apparently is found only in the very deepest water. Ecological notes and formal descriptions for these species were presented by Kawakatsu (1965, 1968, 1973). He stated (1968:15) that they ". . . are the first recorded true lake-dwelling planarians in the United States." Kawakatsu (1968) named the Lake Tahoe species *Phagocata nivea tahoena* and *Dendrocoelopsis hymanae*. However, Kenk (1970) collected additional specimens of *Phagocata* from Lake Tahoe in 1967 and 1968 and, based on morphological differences between these and *P. nivea*, concluded that *tahoena* merited the rank of a separate species. He maintained that there is hardly any close taxonomic relationship between the two species and, "From an evolutionary standpoint it would also seem to be somewhat paradoxical to have an unpigmented surface species (*P. nivea*) closely related to a

Table 4. A check list of the macrobenthos collected from Lake Tahoe, 1962-1963.

Phylum Platyhelminthes
Class Turbellaria
Order Tricladida
Family Planariidae
01. *Phagocata tahoena* Kawakatsu*
Family Dendrocoelidae
02. *Dendrocoelopsis hymanae* Kawakatsu*
Phylum Nematoda
Class Adenophorea
Order Enoplida
Family Mononchidae
03. *Cobbonchus pounamua* Clark
Family Mermithidae
04. *Hydromermis* sp. or *Gastromermis* sp. (or perhaps a new genus)
Phylum Annelida
Class Clitellata
Order Lumbriculida
Family Lumbriculidae
05. *Rhynchelmis rostrata* (Eisen)
06. *Kincaidiana freidris* Brinkhurst and Cook
Order Haplotaxida
Family Tubificidae
07. *Spirosperma beetoni* (Brinkhurst)*
08. *Limnodrilus hoffmeisteri* Claparède
09. *Varichaetadrilus minutus* (Brinkhurst)*
10. *Ilyodrilus frantzi typica* Brinkhurst
11. *Rhyacodrilus brevidentatus* Brinkhurst*
12. *Rhyacodrilus sodalis* (Eisen)
Family Naididae
13. *Arcteonais lomondi* (Martin)
14. *Uncinais uncinata* (Ørsted)
Family Haplotaxidae
15. *Haplotaxis* sp.
Class Hirudinea
Order Pharyngobdellida
Family Erpobdellidae
16. *Helobdella stagnalis* (Linnaeus)
17. *Erpobdella punctata* (Leidy)
Phylum Arthropoda
Class Crustacea
Order Cladocera
Family Sididae
18. *Latona setifera* (O.F. Müller)
Family Daphnidae
19. *Daphnia rosea* Sars
20. *Daphnia pulex* Leydig
21. *Simocephalus serrulatus* (Koch)
Family Bosminidae
22. *Bosmina longirostris* (O.F. Müller)
23. *Drepanothrix dentata* Eurén
Family Macrothricidae
24. *Ilyocryptus acutifrons* Sars
25. *Eurycercus lamellatus* (O.F. Müller)
26. *Camptocercus rectirostris* Schödler
27. *Acroperus harpae* Baird
28. *Alona affinis* (Leydig)
29. *Alona quadrangularis* (O.F. Müller)
30. *Pleuroxus denticulatus* Birge
31. *Chydorus latus* Sars
32. *Chydorus sphaericus* (O.F. Müller)
Order Podocopa
Family Cypridae
33. *Candona tahoensis* Ferguson*
Order Eucopepoda
Family Temoridae
34. *Epischura nevadensis* Lilljeborg
Family Diaptomidae
35. *Leptodiaptomus tyrrelli* (Poppe)
Family Cyclopidae
36. *Acanthocyclops vernalis* (Fischer)
37. *Macrocyclops albidus* (Jurine)
Order Amphipoda
Family Talitridae
38. *Hyalella azteca* (Saussure)
Family Gammaridae
39. *Stygobromus tahoensis* Holsinger*

Table 4. Continued.

- 40. *Stygobromus lacicolus* Holsinger*
- Class Arachnoidea
  - Order Hydrachnellae
    - Family Lebertiidae
      - 41. *Lebertia* sp.
    - Family Hydrovolziidae
      - 42. *Hydrovolzia* sp.
    - Family Hygrobatidae
      - 43. *Hygrobates* sp.
    - Family Limnesiidae
      - 44. *Limnesia* sp.
    - Family Pionidae
      - 45. *Piona* sp.
- Class Insecta
  - Order Plecoptera
    - Family Capniidae
      - 46. *Capnia lacustra* Jewett*
      - 47. *Utacapnia tahoensis* (Nebeker and Gaufin)*
    - Family Nemouridae
      - 48. *Nemoura* sp. ?
    - Family Perlidae
      - 49. *Acroneuria* sp.
  - Order Ephemeroptera
    - Family Siphlonuridae
      - 50. *Siphlonurus* sp.
    - Family Baetidae
      - 51. *Callibaetis* sp.
      - 52. *Centroptilum* sp.
    - Family Heptageniidae
      - 53. *Heptagenia* sp.
    - Family Leptophlebiidae
      - 54. *Choroterpes* sp.
      - 55. *Paraleptophlebia* spp. of the *packi, bicornuta, zayante,* and *helinae* groups (may include a new species)
    - Family Tricorythidae
      - 56. *Tricorythodes fallax* Traver
  - Order Odonata
    - Family Gomphidae
      - 57. *Gomphus kurilis* Hagen
  - Order Trichoptera
    - Family Hydroptilidae
      - 58. *Hydroptila* sp.
    - Family Limnephilidae
      - 59. *Limnephilus* sp.
  - Order Coleoptera
    - Family Dytiscidae
      - 60. *Hydroporus striatellus* LeConte
      - 61. *Agabus disintegratus* Crotch
      - 62. *Colymbetes rugipennis* Sharp
    - Family Hydrophilidae
      - 63. *Tropisternus ellipticus* LeConte
      - 64. *Laccobius ellipticus* LeConte
  - Order Diptera
    - Family Ceratopogonidae
      - 65. *Palpomyia* sp.
    - Family Chironomidae
      - 66. *Conchapelopia* sp.
      - 67. *Ablabesmyia monilis* (Linnaeus)
      - 68. *Apsectrotanypus* possibly *florens* (Johannsen)
      - 69. *Psilotanypus bellus* ? (Loew)
      - 70. *Pseudodiamesa pertinax* (Garrett)
      - 71. *Monodiamesa bathyphila* (Kieffer)
      - 72. *Heterotrissocladius oliveri* Saether
      - 73. *Paratrichocladius* sp.
      - 74. *Orthocladius obumbratus* (Johannsen)
      - 75. *Cryptochironomus* near *fulvus* (Johannsen)
      - 76. *Paracladopelma* near *nais* Townes
      - 77. *Paracladopelma* sp.
      - 78. *Polypedilum* near *scalaenum* (Schrank)
      - 79. *Polypedilum parascalaenum* ? Beck
      - 80. *Pseudochironomus pseudoviridus* (Malloch)
      - 81. *Endochironomus* near *nigricans* (Johannsen)
      - 82. *Stictochironomus* sp.
      - 83. *Phaenopsectra* near *profusa* Townes
      - 84. *Dicrotendipes* near *modestus* (Say)

Table 4. Continued.

85. *Cladotanytarsus* sp. No. 1
86. *Cladotanytarsus* sp. No. 2
87. *Rheotanytarsus* sp.
88. *Tanytarsus* sp.
89. *Tanytarsus* near *guerlus* (Roback)

Phylum Mollusca
Class Pelecypoda (Bivalvia)
Order Veneroida
Family Sphaeriidae
90. *Pisidium* sp.

Class Gastropoda
Order Basommatophora
Family Lymnaeidae
91. *Fossaria bulimoides* (Lea)
Family Physidae
92. *Physella virgata* (Gould)
Family Planorbidae
93. *Helisoma newberri* (Lea)
94. *Vorticifex effusus* (Lea)
Family Ancylidae
95. *Ferrissia fragilis* (Tryon)

* Species endemic to Lake Tahoe.

pigmented subspecies inhabiting the bottom of a deep lake" (Kenk 1970:28). The dorsal surface of living *P. tahoena* is a light hue of grayish brown, becoming lighter towards the margins of the body. The ventral surface is unpigmented, as are two small areas adjoining the eyes and a crescent-shaped rim along the margins of the body (Kenk 1970).

*Phagocata tahoena* was far more abundant and widespread in the bottom samples than *Dendrocoelopsis hymanae*. The former was collected from 1.5 to 497 m and was present in all transects. Kawakatsu (1968) expressed surprise that *Phagocata* was so abundant as to be collected in an Ekman grab. Densities of *P. tahoena* generally exceeded 100/m$^2$ at >30 m and approximated 50/m$^2$ at <30 m, except for low densities (<10/m$^2$) in very shallow water (1-2 m). Kenk (1970) collected large numbers of *P. tahoena* at 40, 69, and 89 m. *Phagocata tahoena* were generally 6 mm long and about 1 mm wide when living (Kenk 1970) and usually 5-8 mm long and 0.7-1.0 mm wide when preserved, with the largest specimens measuring up to 12 mm in length (Kawakatsu 1968).

*Dendrocoelopsis hymanae* was much less common than *Phagocata tahoena*. Of about 250 specimens examined by Kawakatsu (1965), only two were *Dendrocoelopsis*. It is an unpigmented, eyeless species that, in the preserved state, measures up to 14 mm long and about 2 mm wide. In his revision of this genus, Kenk (1973) presented a detailed description of *D. hymanae*.

Studies reported by the CDWR[4] (1966) and Goldman (1974) listed other species of Turbellaria. The former listed a specimen of *Planaria* and the latter a specimen of *Rhynchoscolex*.

*Nematoda*

The only genus positively identified by B.G. Chitwood of Western Washington State College (20 May 1964 letter) was *Cobbonchus*, probably *C. pounamua*, which appeared in grab samples from McKinney Bay and South Lake Tahoe. Specimens

taken at Cave Rock and Crystal Bay were closely related to the genera *Hydromermis* or *Gastromermis*, but may be an undescribed genus. McGauhey et al.[3] (1963) collected nematodes in bottom samples at 2, 4, and 126 m. They were identified only to order Tylenchida. Nematodes were collected in shallow water during the CNF Study (CDWR[4] 1967, 1969, 1970), and Goldman (1974) found three genera in benthos samples from Lake Tahoe: *Trilobus, Dorylaimus*, and *Iotonchus*. Flint[5] (1975) listed the same genera noted by Goldman, and reported three additional ones: *Monochus, Triphyla*, and *Alaimus*.

*Oligochaeta*

Initial identification of oligochaetes was performed by R.O. Brinkhurst of the University of Liverpool, England (11 March 1964 letter). Concerning this material, Brinkhurst (1965:118) stated, "One of the most significant collections obtained is that from Lake Tahoe (California/Nevada), one of the world's deepest lakes, which seems to have many species not known from other localities, several of which pose difficult problems of generic status." The taxonomy of the Lake Tahoe oligochaetes has been elucidated (Brinkhurst 1965, 1981, 1987; Brinkhurst and Cook 1966; Brinkhurst and Jamieson 1971; Loden 1978). The following species are recognized along with limited information on their distribution in Lake Tahoe: *Rhynchelmis rostrata* (unknown), *Kincaidiana freidris* (unknown), *Spirosperma beetoni* (widespread), *Limnodrilus hoffmeisteri* (fairly common), *Varichaetadrilus minutus* (mainly littoral), *Ilyodrilus frantzi typica* (common), *Rhyacodrilus brevidentatus* (90-495 m), *Rhyacodrilus sodalis* (30-495 m), *Arcteonais lomondi* (15-30 m), *Uncinais uncinata* (< 30 m), and *Haplotaxis* sp. (unknown).

Strongly localized distributions of oligochaetes are rare, except for groundwater species and species restricted to known centers of endemicity (Brinkhurst and Jamieson 1971). Lake Tahoe, along with Lake Baikal, several Balkan lakes, and Lake Titicaca, were included among the more significant centers of endemism. Endemic to Lake Tahoe are *Spirosperma beetoni*, *Varichaetadrilus minutus*, and *Rhyacodrilus brevidentatus*. *Kincaidiana freidris* and *Ilyodrilus frantzi* were originally considered endemic as well.

Brinkhurst and Jamieson (1971) cautioned that the supposed endemics of lakes Tahoe and Titicaca may prove to be more widely distributed when the adjacent areas are studied in more detail. They observed that *Ilyodrilus frantzi* has since been found in Lake Washington (Washington State) and probably occurs in other waters as well. In addition, Erman and Erman (1975) reported *Kincaidiana freidris* from several small fens (minerotrophic peatlands): one area near Sagehen Creek, about 24 km northwest of and in the same Lahontan drainage basin as Lake Tahoe, and the other near the coast at Fort Bragg, about 309 km west of Lake Tahoe. They remarked that the macroinvertebrate fauna of the fens ". . . is striking because of its similarities to lake benthos, especially [that of] oligotrophic lakes, in composition and production" (Erman and Erman 1975:602). However, no other species appeared in common with those from Lake Tahoe.

Other macrobenthos sampling programs reported a plethora of oligochaetes and attempted identifications to the generic level. McGauhey et al.[3] (1963) reported *Limnodrilus* and *Pristina* plus four unidentified genera. Only *Pristina* was reported by the CNF study (CDWR[4] 1966). Goldman (1974) listed ten genera: *Peloscolex, Lumbriculus, Limnodrilus, Henlea, Ilyodrilus, Rhynchelmis, Haplotaxis, Naidium* (*Breviseta*), *Eiseniella,* and *Aeolosoma.* Flint[5] (1975) found *Lumbriculus, Peloscolex, Henlea,* and *Xironogiton.*

*Hirudinea*

The freshwater leeches were identified by M.C. Meyer of the University of Maine (March 1965 letter). Specimens collected by hand from very shallow (<0.3 m) water were *Erpobdella punctata,* whereas those recovered from grab samples at 4.9-82 m were *Helobdella stagnalis.* Specimens of *Helobdella* in a retracted or semiretracted state ranged in length from 1.5 to 4.5 mm. Two 4.5-mm individuals had nine and four young (about 1 mm long) attached to their ventral surfaces. Fifty-five of the 62 leeches collected in the benthic sampling came from the South Lake Tahoe transects. The CNF Study recorded leeches off Tahoe Keys only (CDWR[4] 1970, 1971). McGauhey et al.[3] (1963) found leeches in two samples only; one at a depth of 2 m and the other at 154 m, both off Tahoe Keys.

*Illinobdella moorei* were not collected from the benthos, but rather were found attached to the dorsal fins of tui chubs, *Gila bicolor,* which are commonly afflicted with this parasite. In his revision of the leeches of North America, Klemm (1982) recognizes *Helobdella stagnalis,* synonymizes *Illinobdella moorei* with *Myzobdella lugubris,* and uses the trinomial *Erpobdella punctata punctata.*

*Cladocera*

Lake Tahoe cladocerans taken by the Ekman grab were identified by R.W. Kiser of Centralia College, Washington (5 April 1963 and 8 June 1964 letters). He identified the following 15 species (followed by comments regarding relative abundance and distribution): *Latona setifera* (scarce, 6-81 m), *Daphnia rosea* (Emerald Bay, common), *Daphnia pulex* (common, widespread), *Simocephalus serrulatus* (scarce, 29-30 m), *Bosmina longirostris* (common, widespread), *Drepanothrix dentata* (infrequent, 6-21 m), *Ilyocryptus acutifrons* (scarce, 5-7 m), *Eurycercus lamellatus* (common, 1.2-143 m), *Camptocercus rectirostris* (scarce), *Acroperus harpae* (scarce, 1.2-1.8 m), *Alona affinis* (widespread, shoreline to 30 m), *Alona quadrangularis* (scarce, 21 m), *Pleuroxus denticulatus* (scarce, 1.2-1.8 m), *Chydorus latus* (infrequent, shoreline to 7.6 m), and *Chydorus sphaericus* (scarce, 1.2-1.8 m). Although they are widely recognized as planktonic rather than epibenthic species, *Daphnia rosea, D. pulex,* and *Bosmina longirostris* are listed because they appeared in the Ekman grab samples.

Other investigators reported collecting cladocerans in grab samples and in plankton hauls taken in the littoral and limnetic zones of Lake Tahoe. For example, in his pioneering studies at Lake Tahoe in 1904, Juday (1907) found *Daphnia pulex*

(var. *pulicaria*) and *D. hyalina* (var. *richardi*) in the limnetic zone and the following species in the littoral zone: *Ilyocryptus acutifrons, Eurycercus lamellatus, Acroperus harpae, Alona affinis*, and *Chydorus sphaericus*. Kemmerer et al. (1923) reported that the limnetic cladocera included both *Daphnia pulex* and *D. longispina* var. *hyalina*, form *richardi*. Neither McGauhey et al.[3] (1963) nor Goldman (1974) listed cladocerans among the invertebrates taken in bottom samples. However, the latter study listed, among the zooplankters, the same 15 species we collected. Flint[5] (1975) identified *Bosmina* and *Macrothrix* from his benthos samples. Although cladocerans were not listed among the bottom invertebrates collected during the CNF Study, plankton sampling in the littoral and limnetic zones yielded *Alona* sp., *Bosmina coregonii, Chydorus sphaericus, Daphnia rosea, Drepanothrix dentata*, and *Ilyocryptus sordidus* (CDWR[4] 1966, 1967, 1969, 1970, 1971, 1972). Richerson[6] (1969) identified *Daphnia pulicaria, D. rosea*, and *Bosmina longirostris* in the Lake Tahoe zooplankton. He concurs with J. Hrbacek (Hydrobiological Laboratory of the Czechoslovakian Academy of Science, pers. comm.) that the *Daphnia pulex* in Lake Tahoe is actually a separate species, *D. pulicaria*.

*Ostracoda*

The endemic, free-living ostracod, *Candona tahoensis*, described by Ferguson (1966), is abundant and widespread in Lake Tahoe at all depths. We measured ostracods from 0.5-1.5 mm in length. Of his specimens, Ferguson (1966:318) noted, "Overall length 1.44 to 1.46 mm, maximum height 0.75 to 0.78 mm." He also observed that males were equal in size and number to females and greatly resembled them. Goldman (1974) found that *Candona* was the third most dominant benthic organism, comprising about 17% of the total organisms collected. McGauhey et al.[3] (1963) identified *Limnocythere* and *Herpetocyris* in bottom samples. *Candona* was abundant in Flint's[5] (1975) samples.

*Copepoda*

Copepods collected in the 1962 Ekman grab samples were identified by M.S. Wilson of the United States Public Health Service (18 March 1963 letter). They consisted of *Cyclops vernalis, Macrocyclops albidus, Epischura nevadensis*, and *Diaptomus tyrrelli*. *Diaptomus tyrrelli* is now recognized as *Leptodiaptomus tyrrelli* and *Acanthocyclops vernalis* is preferred over *Cyclops vernalis* (J.W. Reid, The Smithsonian Institution, 24 August 1992 letter). Samples that we collected in 1963 and sent to Wilson were lost; an unfortunate circumstance, because they included forms quite distinct from the four named above. *Epischura nevadensis* and *Leptodiaptomus tyrrelli* were abundant in the limnetic zone and appeared in samples of the benthos from the shallows to about 30 m. The copepods found on the bottom in deeper waters were mostly *Acanthocyclops vernalis* and *Macrocyclops albidus*.

[6] Richerson, P.J. 1969. Community ecology of the Lake Tahoe plankton. Ph.D. Dissertation, University of California, Davis, California, USA.

Some of the earlier limnological studies at Lake Tahoe refer to copepods, usually in terms of their presence in the limnetic zone. In what is believed to be the first description, Ward (1904) referred to collections of *Epischura nevadensis* from Lake Tahoe. Juday (1907) identified certain rotifers, copepods, and cladocerans from plankton hauls made in 1904. The copepods were *Epischura nevadensis* and a species of *Diaptomus*. Kemmerer et al. (1923) apparently collected the same species during the summer 1913.

McGauhey et al.[3] (1963) found both harpacticoid and cyclopoid copepods in bottom samples at Lake Tahoe. Goldman (1974) listed *Diaptomus tyrrelli* and *Epischura* among the organisms found in the benthos samples. However, his list of copepods found in the zooplankton also included the four species listed in Table 4 plus the harpacticoid copepod, *Bryocamptus zschokkei*. From his benthos samples, Flint[5] (1975) recovered *Diaptomus, Bryocamptus*, and *Cyclops*. *Epischura* was the only copepod listed among the bottom-dwelling invertebrates taken during the CNF Study. Plankton sampling in the littoral and limnetic zones, however, yielded *Epischura nevadensis, Diaptomus tyrrelli, Diaptomus* sp., *Cyclops* sp., *Mesocyclops* sp., and undescribed harpacticoid specimens (CDWR[4] 1966, 1967, 1969, 1970, 1971, 1972). Students and faculty of the University of California, Davis, have engaged in numerous zooplankton studies at Lake Tahoe. The copepods mentioned by them are *Epischura nevadensis* and *Leptodiaptomus tyrrelli*. These species are planktonic, whereas *Acanthocyclops vernalis* and *Macrocyclops albidus* are epibenthic (J.W. Reid, 24 August 1992 letter). Nevertheless, any species taken in the bottom grabs were listed in Table 4.

*Amphipoda*

Amphipods or scuds are very abundant and widespread in Lake Tahoe. They separate into a shallow-water form, represented by *Hyalella azteca*, and two endemic deep-water forms, represented by *Stygobromus tahoensis* and *S. lacicolus*. The two genera do not overlap in distribution. *Hyalella* is concentrated in the littoral zone with none collected beyond the 30 m depth. *Stygobromus* is uncommon between 30 and 60 m, but plentiful from 60 m to the greatest depth sampled (501 m).

L. Hubricht of Meridian, Mississippi, made the initial identification of the amphipods (18 June 1962 and 8 July 1965 letters). The more shoreline oriented of the littoral scuds was described as *H. azteca* and those taken at 5-30 m were called *Hyalella inermis*. The species from very deep water was termed *Stygobromus hubbsi*, or a species very close to it. *Stygobromus hubbsi* is a species originally described from Malheur Cave in Oregon. It was on these determinations that Frantz and Cordone (1966) listed *H. azteca, H. inermis*, and *S. hubbsi*. Holsinger (1974) pointed out, however, that *H. inermis* is usually regarded as a synonym of *H. azteca*.

Final identification of the endemic Lake Tahoe amphipods was made by Holsinger (1974). The predominantly subterranean amphipod genus *Stygobromus* is, with a single exception, restricted to North America. With the exception of those found in Lake Tahoe, the western species inhabit subterranean biotopes, including limestone and lava caves, wells, and springs. The two endemic Lake Tahoe species

are *S. tahoensis* and *S. lacicolus*. "The records . . . are the first reported occurrences for blind, white amphipods from a deep, oligotrophic lake in the United States" (Holsinger 1974:44).

We were unable to distinguish the two species of *Stygobromus* at the time collections were made. The only information available on the relative distribution and abundance of the two species is based on material examined by Holsinger (1974). He reported that 13 samples contained 550 *S. tahoensis*, whereas only 11 *S. lacicolus* were recovered from five samples. Three of the five held only *S. lacicolus* and two held both species. The *S. tahoensis* specimens were taken at 66-495 m, with Emerald Bay samples ranging from 35 to 60 m. *Stygobromus lacicolus* specimens were collected from depths between 60 and 355 m. The substrate preference of *Stygobromus* in Lake Tahoe is not strictly associated with the deep-water plant zone; they are abundant from 60 m to the lake bottom at 501 m, whereas the plants are most concentrated at 61-107 m (Frantz and Cordone 1967).

Specimens of *H. azteca* were generally from 1 to 3 mm long (maximum 5 mm). Most *Stygobromus* specimens were <6 mm long; the largest was a 9-mm specimen taken at 472 m. Eggs per female ranged from one to eight and were present during all months of sampling. Egg numbers are underestimated since they are readily lost during sample processing. Of the 550 specimens of *S. tahoensis* examined by Holsinger (1974:44) ". . . 51 were ovigerous females ranging in size from 3.8 to 6.5 mm ($\bar{x}$ = 4.8 mm). The number of eggs and/or embryos per female ranged from 1 to 5 ($\bar{x}$ = 2.25). Ovigerous females were found in samples taken during May, July, August, September, October, and December. Males and juveniles were also found in most of these samples, but females were always the most abundant." The largest male was 5.0 mm. He also observed that, of the 11 specimens of *S. lacicolus*, eight were males, two were juveniles, and one was a female; the largest male was 5.5 mm and the female was 6.0 mm.

Other bottom sampling efforts recorded the presence of amphipods in Lake Tahoe. The information generally confirms what is presented here; however, *Crangonyx* sp. was reported by Flint[5] (1975) and by the CNF Study (CDWR[4] 1966, 1967, 1970).

*Acari*

Aquatic mites were identified by R. Mitchell of the University of Michigan (19 March 1963 letter). Five genera are represented, but species determinations are lacking. He was surprised to find *Hydrovolzia* in deep water, since it is usually thought of as a relict form limited to cold springs and, occasionally, cold streams. He found the combination of genera to be very peculiar since, except for the presence of *Piona*, the samples would appear to be from a stream, not a lake.

General comments on the distribution of the mite genera are based on Mitchell's identifications of a series of mite samples. Both *Lebertia* and *Hydrovolzia* were widely distributed in Lake Tahoe, with the former found to 60 m and the latter apparently restricted to depths between 30 and 123 m. *Hygrobates* was taken from the McKinney Bay transect down to 17 m, whereas *Limnesia* occurred in scattered

samples to 29 m or more. *Piona* was not abundant and was restricted to <30 m.

Water mites were given only casual mention in reports describing other investigations of the Lake Tahoe benthos. Flint[5] (1975) reported the presence of *Lebertia* in his samples. Goldman (1974) listed a specimen of *Limnochares* among the invertebrates collected.

*Plecoptera*

Stonefly nymphs, which are widespread in Lake Tahoe, include two unusual endemic species and at least two common genera. The endemic species are represented by a deep-water and a shallow-water form in which both sexes are wingless throughout their life span.

S.G. Jewett, Jr., of the United States Fish and Wildlife Service, described the deep-water species as *Capnia lacustra* (Jewett 1965). In his 24 June 1962 letter, Jewett stated, "This species is very interesting and it is almost incredible that it lives at depths in Lake Tahoe." It is most abundant from 60 to 110 m, apparently in close association with beds of *Chara*, moss, and filamentous algae. The maximum depth recorded for this species was 274 m in McKinney Bay. The shallow-water species was originally described as *Capnia tahoensis* by Nebeker and Gaufin (1965), but was given generic status, *Utacapnia tahoensis*, by Zwick (1973). Emerging adults were collected from exposed rocks at the water's edge just south of Sand Harbor in April 1964. Body lengths of *Utacapnia tahoensis* reported by Nebeker and Gaufin (1965) ranged from 4.9 to 5.1 mm for males and from 5.9 to 6.1 mm for females.

The deep-water form was so unusual that it was considered worthy of a brief note in *Science* (Jewett 1963). It was believed previously that representatives of only the Coleoptera, Hemiptera, and Diptera were adapted in both adult and immature stages for living in water. Ordinarily, the adults of aquatic insects are terrestrial. "Therefore, it is of considerable interest to record the discovery of a species of stonefly (Plecoptera) that evidently passes its entire life history at some depth in Lake Tahoe . . ." (Jewett 1963:484). No external gills are present in either the nymphs or adults so the means by which these stoneflies secure oxygen is unknown. Jewett (1963:484) surmised that they may ". . . acquire oxygen by absorption through the body covering as they crawl among the plants growing on the lake bottom."

Baumann (1979:66) also commented on its uniqueness; i.e., "Another example of restricted distribution in the stoneflies is *Capnia lacustra* Jewett, which only occurs in Lake Tahoe. It carries on its entire life cycle under water at depths of 100-400 feet . . . Only one other similar stonefly is known, and that is the genus *Baikaloperla* . . . in Lake Baikal, Siberia. It is also wingless and possesses similar morphological and ecological traits. It is not surprising that these two deep, ancient lakes contain similar rare species which evolved under specialized conditions and will be lost if their habitat is destroyed."

*Capnia lacustra*, like other species of *Capnia*, is a small stonefly. The largest specimen was 6 mm long, and the body lengths of those examined by Jewett (1965) ranged from 4.5 to 5.5 mm. Pigmentation in this species is apparently more limited than in other members of the genus (Jewett 1963).

The unusual wingless state of the endemic Lake Tahoe stoneflies may be correlated with environmental conditions. Brinck (1949:172-175) speculated that the unrestricted wind typical of large bodies of water could be a significant factor by blowing flying forms away from the lake, thus making flight disadvantageous.

A very small stonefly nymph collected in 4.9 m of water off Tahoma was identified by Jewett (4 April 1964 letter) as ". . . likely a species of *Nemoura*," but he was not absolutely sure. The remaining genus, *Acroneuria,* was collected along the shoreline at Sugar Pine Point.

Other studies made brief mention of stoneflies. *Capnia*, probably *U. tahoensis*, were recorded by Flint[5] (1975). They were also found in artificial substrate cages at widely scattered shallow water locations around Lake Tahoe (CDWR[4] 1967, 1969, 1970). This same investigation reported the capture of five *Alloperla* specimens from a cage off the mouth of the Upper Truckee River (CDWR[4] 1969).

*Ephemeroptera*

Mayflies are common in the shallow waters of Lake Tahoe. Seven genera, including one identified to the species level, were verified by G.F. Edmunds, Jr., of the University of Utah (7 May 1964 letter) (Table 4). Specimens were collected in the 1-2-m zone and several were found between 5 and 10 m in McKinney Bay and in Crystal Bay. Ten were recovered from one grab sample taken in 1.2 m in McKinney Bay. The depth record is represented by a single specimen recorded at 7 m in Crystal Bay.

Since no special effort was made to sample rubble and rocky substrates, very shallow water (<1 m), or mouths of tributaries, our list of Lake Tahoe mayflies is likely incomplete. This conclusion is supported by the CNF Study (CDWR[4] 1966, 1967, 1969, 1970, 1971). Mayfly nymphs were common in artificial substrate cages, comprising as much as 4% of the total number of organisms collected. The cages yielded a greater variety and number of mayflies than the grab samples. The following mayfly genera were identified by the CNF Study: *Ameletus*, *Baetis*, *Caenis*, *Callibaetis*, *Centroptilum*, *Choroterpes*, *Cinygmula*, *Ephemerella*, *Heptagenia*, *Ironodes*, *Leptophlebia*, *Paraleptophlebia*, *Potamanthus*, and *Tricorythodes.*

*Odonata*

Two dragonfly nymphs were sent to L.K. Gloyd of the Illinois Natural History Survey for identification. In her 30 March 1964 letter, she assigned them to *Gomphus kurilis* but observed that *G. donneri*, *G. kurilis*, and *G. sobrinus* may all be synonyms of *G. confraternus*. The specimens were taken from shallow water in Emerald Bay. A more intensive search of Lake Tahoe shallows probably would reveal additional dragonfly species.

*Hemiptera*

The only hemipteran recorded was a single specimen of *Lethocerus americanus* taken by hand near the mouth of Burton Creek. It was collected and identified by the senior author.

*Megaloptera*

A single alderfly larva was found in the stomach of a lake trout collected on 21 May 1983 by the senior author. It was identified as *Sialis occidens* by M.F. Whiting of Cornell University. In his 22 August 1992 letter, he noted that, "The larvae of this species and *S. californica* are identical but only *occidens* is known from Tahoe."

*Trichoptera*

Caddisfly larvae were identified by D.G. Denning of Moraga, California (19 April 1964 letter) (Table 4). Those identified were collected from shallow water. A specimen of *Limnephilus* was collected by grab between 3 and 7.6 m off the mouth of Blackwood Creek, and a specimen of *Hydroptila* was taken from 0.3 m in Glenbrook Bay. An early instar member of the family Leptoceridae was recovered at 4.9 m off Camp Richardson. What appeared to be occasional caddisfly cases, larvae, or pupae were sampled from deeper water (19, 22, 64, 65, and 123 m), but confirmation by an expert is lacking. The senior author identified a specimen of *Hesperophylax* taken by hand in shallow water at Lake Forest.

Ekman grab sampling and the limited collecting in shallow rubble areas probably underestimate the abundance and diversity of caddisflies in Lake Tahoe. They were occasionally taken in grab samples and the artificial substrate cages utilized in the CNF Study (CDWR[4] 1966, 1967, 1969, 1970, 1971). As with mayflies, caddisflies were more abundant in the cage than in the grab samples. A specimen of *Mystacides* was found at 7.6 m and psychomiids reported from 6 and 9 m. *Hydroptila* was common in the cage samples set in shallow water. The following caddisfly genera were reported by the CNF Study: *Hydroptila*, *Mystacides*, *Ochrotrichia*, *Oxyethira*, *Polycentropus*, and *Psychomyia*.

*Coleoptera*

I. La Rivers of the University of Nevada, Reno, identified the aquatic beetles (Table 4). All specimens were taken by hand in shallow water near the mouth of Burton Creek, except for a specimen of *Colymbetes rugipennis* taken in a grab in Emerald Bay. An unidentified beetle larva (7 mm long) was collected from 482 m with the 22.9-cm Ekman grab. A riffle beetle larva (family Elmidae) was collected at about 3 m off Tahoe Keys (CDWR[4] 1971).

*Diptera*

Dipteran larvae were identified by S.S. Roback of the Philadelphia Academy of Natural Sciences (28 May 1965 letter) and scientific names were updated by W.P. Coffman of the University of Pittsburgh in January 1993 (Table 4). Numerous species make up the dipteran fauna of Lake Tahoe, but in many instances identification to species is uncertain. The following information is available on the distribution and relative abundance of the different taxa collected: *Palpomyia* sp. (one specimen from Emerald Bay), *Conchapelopia* sp. (one from McKinney Bay), *Ablabesmyia monilis* (one from South Lake Tahoe), *Apsectrotanypus* possibly *florens* (infrequent, McKinney Bay), *Psilotanypus bellus*? (widespread, but not abundant, <30 m), *Pseudodiamesa pertinex* (scarce), *Monodiamesa bathyphila* (widespread, >30 m), *Heterotrissocladius oliveri* (widely distributed), *Paratrichocladius* sp. (infrequent, <150 m), *Orthocladius obumbratus* (scarce), *Cryptochironomus* near *fulvus* (usually <30 m), *Paracladopelma* near *nais* (widespread, >150 m), *Paracladopelma* sp. (primarily restricted to west side and <150 m), *Polypedilum* near *scalaenum* (scarce), *Polypedilum parascalaenum*? (scattered, <150 m), *Pseudochironomus pseudoviridus* (unknown), *Endochironomus* near *nigricans* (widespread to 300 m), *Stictochironomus* sp. (<30 m on west side), *Phaenopsectra* near *profusa* (scarce), *Dicrotendipes* near *modestus* (scarce), *Cladotanytarsus* sp. No. 1 (<150 m on south and west sides), *Cladotanytarsus* sp. No. 2 (infrequent), *Rheotanytarsus* sp. (scarce), *Tanytarsus* sp. (Crystal Bay and South Lake Tahoe, <150 m), and *Tanytarsus* near *guerlus* (scarce). Of the 25 taxa listed above, *Palpomyia* sp. is in the family Ceratopogonidae and the remainder are in family Chironomidae.

Saether (1975a) redescribed *Heterotrissocladius oliveri* and noted that it is listed in Frantz and Cordone (1966) as *Metriocnemus* near *lundbecki*. He observed that *H. oliveri* is strongly cold-stenothermic and ultra-oligotrophic, and that it appears to have relict occurrence in Lake Tahoe. *Pseudochironomus pseudoviridus* was also described from Lake Tahoe (Saether 1977).

Dipteran larvae are a significant component of the Lake Tahoe bottom fauna. McGauhey et al.[3] (1963) and Flint[5] (1975) noted that they were among the more common organisms, but they were identified only as larvae of the family Chironomidae. Only 21 dipteran larvae (2% of the total) were found in the 41 bottom samples collected by Goldman (1974). They were identified as *Phaenopsectra* sp., *Chironomus* (*Atritibia*) sp., *Procladius* sp., and representatives of subfamily Orthocladiinae. About 57 dipteran taxa were identified during the CNF Study (CDWR[4] 1966, 1967, 1969, 1970, 1971). Dipteran larvae were particularly abundant in the artificial substrate cages.

*Pelycypoda*

The freshwater clams were identified by W.J. Clench of Harvard University as *Pisidium* (28 February 1963 letter). The nomenclature of this family was in a very confused state when the clams were identified. Taylor (1981) listed several species of *Pisidium* and *Musculium* which, by reason of their general distribution, might be

found in Lake Tahoe. He cautions, however, that identification of California freshwater mollusks may be difficult because of the numerous undescribed species and even genera, especially among small and inconspicuous forms. We expect, therefore, that a careful study of Lake Tahoe clams will uncover new species. Although not abundant, clams were widespread in Lake Tahoe. They were found in the shallows to a maximum depth of 188 m. The length of most of the clams was 1-3 mm, with a maximum of 4 mm.

Freshwater clams were mentioned in other Lake Tahoe benthic studies. Hanna and Smith (1937) listed *Pisidium* among the invertebrates taken by dredging in relatively deep water. *Musculium* appeared among the list of the invertebrates collected in 1962 at 2 and 72 m (McGauhey et al.[3] 1963). Goldman (1974) and Flint[5] (1975) listed specimens of *Pisidium*. This genus also appeared in the grab samples described by CDWR[4] (1966, 1967, 1969, 1970, 1971). Freshwater mussels were taken from the Rubicon Point area in 1957 by P.A. Mitchell, former State Park Naturalist at the D.L. Bliss State Park. Originally described as *Margaritifera margaritifera*, this species, according to Taylor (1981), should now be known as *Margaritifera falcata*.

*Gastropoda*

Five species of gastropods were identified from material sent to W.J. Clench of Harvard University (28 February 1963 and 31 March 1964 letters)[7]. He also noted a specimen of Hydrobiidae, possibly of the genus *Littoridina*, but so badly corroded to preclude positive determination. He observed that *Ferrissia fragilis* was a new record for Lake Tahoe. He also observed that the shells look as though they had come from a low calcium environment. Robert Hershler of The Smithsonian Institution (21 August 1992 letter) was skeptical about the presence of *Littoridina*: "This is highly unlikely given that this beast thus far is known only from brackish estuaries on both coasts of Central America."

*Physa virgata* was collected by hand from the north end of the lake at 8-30 cm. One specimen of *Ferrissia fragilis* was taken at 7 m in Crystal Bay. *Lymnaea bulimoides* was represented by a few specimens from the Cave Rock area at 6-7.3 m. *Parapholyx effusa* came from >15 m; one from 125 m off Tahoe City represents the depth record. *Parapholyx* specimens were widely distributed with noticeable concentrations at the south end from 21 to 100 m. Nearly all specimens were recovered from plant beds. Specimens of *Carinifex newberryi* were taken most frequently from sand substrates at the south end from 1.5 to 46 m. They were associated with the plant beds also, but to a lesser degree.

Other investigators have studied the gastropods of Lake Tahoe. Baker (1911) identified *Galba bulimoides* from the outlet of Lake Tahoe at Tahoe City. Surprised

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[7] If one follows the most recent list of gastropod scientific names (Turgeon et al. 1988), as we have done in Table 4, then *Physa* should read *Physella*, *Lymnaea* should read *Fossaria*, *Carinifex* becomes *Helisoma*, and *Parapholyx effusa* becomes *Vorticifex effusus*.

by the lack of mollusk records from Lake Tahoe, malacologists from the California Academy of Sciences made a special effort to collect them in October 1933 and August 1936 (Hanna and Smith 1937). Reasoning that the lack of records was due to searches being conducted only along the shoreline, they sampled in relatively deep water, using a dredge to sample to 90 m at two locations in McKinney Bay. In every case beyond 37 m, shells were found among the aquatic plants that came up. They identified *Parapholyx effusa, Carinifex newberryi, Valvata humeralis californica*, and *Lymnaea* sp. They also referred to a report of the remains of *Carinifex newberryi* being found in the stomachs of ducks collected in 1926 and 1927 and claimed that these were the first shells recorded from Lake Tahoe.

The report by Hanna and Smith (1937) prompted van der Schalie and Berry (1948) to describe the gastropods they found in June 1934 living in abundance on a small rocky shoal, apparently near Tahoe City. They felt the collection was worth describing because it consisted almost entirely of littoral pulmonates and thus supplemented the earlier profundal records. They identified *Lymnaea stagnalis wasatchensis*, *Lymnaea bulimoides*, *Gyraulus vermicularis*, and *Physa virgata*. Only dead or badly weathered specimens of *Carinifex newberryi* and *Pompholyx effusa* were found, supporting the habitat preference of these species as shown by Hanna and Smith (1937).

A peculiarity of most specimens of all species collected by van der Schalie and Berry (1948) was the costate sculpturing of the shells. They suggested that the pronounced ridges may be brought about by an unfavorable environment; e.g., some chemical factor in the water or a physical characteristic such as extreme temperature fluctuations in the shallow water during the growing season.

McGauhey et al.[3] (1963) reported a specimen of *Menetus* sp. from a grab sample at 72 m off Tahoe Keys, and Goldman (1974) listed one specimen each of *Parapholyx* and *Gyraulus*. The latter genus was reported by Flint[5] (1975). Snails were common in the grab samples taken during the CNF Study (CDWR[4] 1966, 1967, 1969, 1970, 1971). The following taxa were reported: *Carinifex, Valvata, Parapholyx, Gyraulus*, and a member of family Amniocolidae. *Carinifex* apparently was the most common form, and the snails occurred most frequently at the south end of the lake off Taylor Creek and the Upper Truckee River.

## DISCUSSION

### Lake Typology

The species composition of the macrobenthos collected from Lake Tahoe in 1962 and 1963 reflects oligotrophic conditions. The species of chironomids inhabiting the profundal zone have been used by Saether (1975b) to classify trophic lake types. For example, certain members of the subfamily Orthocladiinae characterize oligotrophic lakes. One species, *Heterotrissocladius oliveri*, is widespread in Lake Tahoe and is considered an indicator of ultra-oligotrophic conditions (Brinkhurst 1974). Along with key physical and chemical features (Goldman 1988), the macrobenthic community of Lake Tahoe is indicative of oligotrophy. Goldman (1983, 1988)

summarized the limnological characteristics of Lake Tahoe that place it among the more ultra-oligotrophic lakes of the world. A comparison of the standing crop of Lake Tahoe macrobenthos with that of other large North American oligotrophic lakes, however, tends to support "moderate" rather than "ultra" oligotrophy for Lake Tahoe.

To compare the mean standing crop of Lake Tahoe macrobenthos with that of other lakes, we converted wet weight to dry weight since almost all other data were reported as dry weight. Dry weight was assumed to be 15% of the wet weight (Beatty[8] 1968). The mean standing crop of the Lake Tahoe bottom fauna approximates 9 kg/ha dry weight. This is higher than 18 of the other 21 oligotrophic lakes listed in Table 5, and in 16 of these the mean weight is <5 kg/ha. Also, special conditions account for the two highest standing crops listed. The >44 kg/ha figure for Lake Winnipeg may be due to its relatively shallow configuration and the presence of an unusually dense population of burrowing mayfly nymphs of genus *Hexagenia* (Rawson 1953). The atypically high bottom fauna population in Paul Lake is the result of a warm epilimnion and a highly productive *Chara* zone (Rawson 1942).

Brinkhurst (1974) examined data from four sets of North American lakes and found that the standing crop of the benthos was inversely related to mean depth and area and directly related to total dissolved solids (TDS). With its large size, great mean depth, and low TDS, one might have predicted a much lower standing crop for Lake Tahoe than the estimated 9 kg/ha. However, our estimate for Lake Tahoe may be biased upwards due to sampling error, particularly the relatively small number of samples taken from deep water, and problems associated with the assumption that standing crop is proportional to production.

Unusually light predation on deep-water invertebrates such as *Stygobromus* may be involved. The low density of fish of any species at >150 m (California Department of Fish and Game, unpublished data) accounts for the belief that invertebrate mortality from fish predation is of minor importance. Several investigations (reviewed by Brinkhurst 1974) demonstrated that fish predation can depress populations of bottom-dwelling invertebrates. Since about 75% of the total surface area of Lake Tahoe exceeds the 150 m depth contour, the atypically high bottom fauna densities in this portion of the lake may account for the high standing crop of Tahoe benthos relative to that of other oligotrophic lakes. R.C. Richards of the Tahoe Research Group (14 August 1992 letter) suggested two other possible reasons for the relatively high standing crop estimates: "Another source of high estimates on standing crop may be that other researchers don't normally count pelagic zooplankton (*Epischura*, etc.) as benthos. Also, oxygen levels are always high in Tahoe and may become seasonally low in other lakes to the point of limiting the success of the benthos. . . "

[8] Beatty, K.W. 1968. An ecological study of the benthos of Castle Lake, California. Ph.D. Dissertation, University of California, Davis, California, USA.

Table 5. Estimated standing crop of macrobenthos for relatively large oligotrophic lakes.

| Lake | Locality | Area (km²) | Mean depth (m) | Mean dry weight (kg/ha) | Reference |
|---|---|---|---|---|---|
| Superior | United States/Canada | 83,300 | 145 | 0.5 | Cook (1975) |
| Great Bear | Northwest Territories | 28,490 | 100 | 0.5 | Larkin (1964) |
| Great Slave | Northwest Territories | 27,200 | 62 | - | Larkin (1964) |
| Main lake | Northwest Territories | - | - | 2.5 | Larkin (1964) |
| East arm | Northwest Territories | - | - | 0.7 | Larkin (1964) |
| Winnipeg | Manitoba | 24,300 | 13 | >44.0 | Larkin (1964) |
| Athabaska | Saskatchewan | 7,700 | 26 | 4.1 | Larkin (1964) |
| Reindeer | Saskatchewan | 5,569 | 17 | 1.6 | Rawson (1960) |
| Wollaston | Saskatchewan | 2,062 | 20.6 | 4.7 | Rawson (1960) |
| La Ronge[a] | Saskatchewan | 1,178 | 12.7 | 8.9 | Rawson (1960) |
| Hunter Bay | Saskatchewan | 129 | 20.7 | 7.1 | Rawson (1960) |
| Cree | Saskatchewan | 1,152 | 14.9 | 1.6 | Rawson (1960) |
| **Tahoe** | **California/Nevada** | **499** | **313** | **8.9** | **This study** |
| Okanagan | British Columbia | 370 | 69.5 | 1.5 | Rawson (1942) |
| Amisk | Saskatchewan | 321 | 13.2 | 9.1 | Rawson (1960) |
| Frobisher | Saskatchewan | 313 | 5.5 | 2.2 | Rawson (1960) |
| Washington | Washington | 88 | 32.9 | 8.0[b] | Thut (1969) |
| Maligne | Alberta | 22 | 40.5 | 2.5 | Rawson (1942) |
| Minnewanka | Alberta | 13 | 38.1 | 3.4 | Rawson (1942) |
| Fish | Utah | 12 | 25.9 | 3.7[c] | Shirley (1972) |
| Waterton | Alberta | 10 | 69.2 | 1.3 | Rawson (1942) |
| Louisa (August) | Ontario | 6 | 19.8 | 1.8 | Wood (1953) |
| Louisa (October) | Ontario | 6 | 19.8 | 2.4 | Wood (1953) |
| Paul | British Columbia | 4 | 34.2 | 27.3 | Rawson (1942) |
| Bow | Alberta | 4 | 17.6 | 1.7 | Rawson (1942) |
| Redrock | Ontario | 3 | 8.8 | 3.1 | Wood (1953) |

[a] Considered mesotrophic by Rawson (1960).
[b] Profundal zone only.
[c] Sublittoral and profundal zones only.

## Endemism

The degree of endemism in the Lake Tahoe invertebrate fauna is not widely recognized. Goldman (1983:28) stated, "The community structure of Lake Tahoe, like most oligotrophic lakes, is simple and because of its relative youth has only evolved a single endemic species (a flightless stone fly)." It appears, however, that Tahoe supports at least 10 species of endemic macroinvertebrates, and further studies may reveal additional endemics. Conversely, it is possible that invertebrate collections in other Sierra Nevada waters (e.g., see Erman and Erman 1975) may demonstrate a more widespread distribution of some of these supposed endemics. Nevertheless, some unusual invertebrate life forms have evolved, which is further reason to protect and preserve this special ecosystem.

## Deep-water Plants

Lake Tahoe is home both to an abundant and varied bottom fauna and a remarkable zone of deep-water aquatic plants (Frantz and Cordone 1967). Crater Lake in Oregon is the only other lake known to support a similar plant community. According to Hasler (1938:95), "The most startling biological finding at Crater Lake was the collection, by dredge, of green mosses, *Fontinalis* and *Drepanocladus*, at the astonishing depth of 394 feet (120 meters). At depths of 60-200 feet, near Wizard Island, these mosses form a mat sufficiently thick to prevent the passage of a 6 inch Ekman dredge through the 'weeds' to the bottom."

The deep-water plant beds in Lake Tahoe do not contain higher vascular plants. Rather, the beds are composed of bryophytes (mosses and liverworts), multicellular algae of the "filamentous" type, and Characeae (stoneworts). The maximum depths recorded for these plants in Lake Tahoe apparently are the deepest ever recorded for any lake (Hutchinson 1975). Because of this, the plant beds and the invertebrates they support have profound ecological significance. Unfortunately, this community is in jeopardy because light transmittance apparently controls the depth distribution of the plants, and water transparency has been decreasing in recent years.

Frantz and Cordone (1967) sampled the deep-water plant beds in 1962 and 1963. Plant densities declined sharply at >100 m, apparently in response to severe light reduction. The condition of *Chara* taken from deep water reflected the controlling influence of light. In a 26 November 1963 letter to P.R. Needham, P.C. Silva quoted R.D. Wood, ". . . it [a sample of *Chara*] is probably a vegetative state of extreme inhibition in cold, dark and deep conditions in Lake Tahoe. Note: totally ecorticate, axial nodes swollen, branchlets reduced and poorly developed, . . ." He also quoted F.K. Daily, "The rest of the material was sterile, ecorticate and of simple construction such as one encounters in the lower whorls of an impoverished, degenerate chara."

Given the continuous loss of transparency since the early 1960s, the deep-water plant beds may have suffered significant reduction. Goldman (1988:132) reported that, "As the population in the Tahoe basin has rapidly increased, Lake Tahoe has been characterized by an increase in primary productivity that has averaged 5.6% $yr^{-1}$ for the last 28 yr. There has been a concomitant decline in transparency of 0.37 m $yr^{-1}$." Should further significant enrichment occur, reduced light penetration might permanently eliminate this unique plant community. It may already be too late for some of the plant beds. The loss of the deep-water plant beds at Lake Tahoe would substantially reduce the lake's biological diversity. These beds constitute an unusual plant and animal community of special scientific interest. They also apparently provide important food and cover for Lake Tahoe fishes and crayfish, and may be vital to the survival of epiphytic invertebrates like the endemic plecopteran, *Capnia lacustra*. Beauchamp et al. (1992) described the successful spawning of lake trout on dense beds of *Chara delicatula* in the southeast region of Lake Tahoe. This was the first example of lake trout spawning on deep-water macrophytes, and is another indication of the importance of this habitat.

The present status of the deep-water plant beds and the epiphytic invertebrates dependent on them is unknown. A species of special concern is the endemic *Capnia lacustra*. Nelson and Baumann (1989:328) stated, "This species has not been collected again despite our intense [sampling] efforts using the facilities of the University of California, Davis Research Station on Lake Tahoe." The sampling effort (22 March 1985) consisted of six bottom trawl hauls for 7-8 min each at depths to 130 m in Carnelian Bay, and seven grabs with the Shipek sampler at 10, 60, 90, and 137 m in Carnelian Bay and off Tahoe City (R.C. Richards, pers. comm.). A systematic survey is needed to quantitatively assess this unique stonefly and the entire deep-water plant community.

## RECOMMENDATIONS

1. Increase efforts to stimulate research on the benthic flora and fauna of Lake Tahoe. Studies of these subjects at Lake Tahoe are extremely scarce, especially when compared with the more classical limnological and fisheries investigations. Sampling and taxonomic difficulties may underlie this deficiency. However, many of these problems can be overcome, and researchers will be rewarded with additional knowledge concerning a fascinating assemblage of plants and animals; organisms that are largely unknown and of great value to science. Also, these plants and animals constitute communities that are fragile and should be sensitive indicators of environmental change.

2. Do not introduce any additional invertebrates into Lake Tahoe. The establishment of *Mysis relicta* in Lake Tahoe has had a profound negative impact on the zooplankton community: the three dominant cladocerans *(Daphnia rosea, D. pulex*, and *Bosmina longirostris*) have virtually disappeared. A considerable literature (summarized by Richards et al. 1991) documents this phenomenon. The effect of *Mysis relicta* on the macrobenthos has not been studied in Lake Tahoe. Other studies (summarized by Northcote 1991), however, have documented predation by this shrimp on amphipods and benthic cladocerans. Spatial overlap at Lake Tahoe can be assumed since SCUBA divers have observed mysids on the bottom at 20-30 m (Rybock[9] 1978). In addition, they have been observed on the bottom at 213 m from a submarine (R.C. Richards, pers. comm.). Mysids probably exist on the bottom in deeper water, but sampling difficulties have precluded the necessary documentation. It is likely that major changes in the Lake Tahoe macrobenthos have resulted from the combination of cultural eutrophication and the introduction of *M. relicta*.

## ACKNOWLEDGMENTS

This study was funded in part by Federal Aid in Sport Fish Restoration Act Projects F-21-R (California) and F-15-R (Nevada). We are particularly grateful to those specialists who made the species identifications; their names are given under

[9] Rybock, J.T. 1978. *Mysis relicta* Lovén in Lake Tahoe: Vertical distribution and nocturnal predation. Ph.D. Dissertation, University of California, Davis, California, USA.

each species group. We also thank D.A. Beauchamp, J.W. Curran, W.A. Dill, L.L. Eng, D.C. Erman, A.C. Knutson, Jr., J.E. Reuter, R.C. Richards, and D.K. Shiozawa for reviewing the manuscript. We are indebted to S. Henry and L. Holmes for typing this paper.

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Received: 2 August 1995
Accepted: 26 March 1996

Appendix 1. Mean estimated number of bottom invertebrates per $m^2$ in Lake Tahoe, California, 1962 (standard deviations are in parentheses).[a]

| Depth range (m) | Samples[b] | Coel | Turb | Olig | Hiru | Ostr | Amph[c] | Zoop | Acar | Plec | Dipt[d] | Pele | Gast |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 5-10 | 31 | 0 | 32 (77) | 1010 (704) | 0 | 162 (254) | 165 (633) | 35 (50) | 22 (71) | 1 (8) | 312 (380) | 14 (42) | 12 (28) |
| 15-30 | 29 | 0 | 46 (114) | 1825 (1020) | 27 (77) | 200 (312) | 49 (121) | 131 (252) | 31 (54) | 12 (50) | 362 (410) | 33 (65) | 212 (961) |
| 60-90 | 32 | 12 (47) | 124 (289) | 1224 (1042) | 5 (18) | 484 (528) | 320 (943) | 32 (56) | 31 (89) | 38 (100) | 153 (235) | 40 (133) | 42 (86) |
| 120-150 | 23 | 0 | 41 (84) | 275 (308) | 0 | 82 (111) | 140 (176) | 19 (29) | 6 (20) | 13 (27) | 47 (100) | 2 (9) | 2 (9) |
| 350-400 | 2 | 0 | 10 (14) | 153 (189) | 0 | 77 (81) | 163 (41) | 10 (14) | 0 | 0 | 19 (27) | 0 | 0 |
| 450-500 | 3 | 0 | 370 (94) | 1461 (650) | 0 | 13 (22) | 938 (297) | 6 (11) | 0 | 0 | 0 | 0 | 0 |
| Total | 120 | | | | | | | | | | | | |

[a] Coel = Coelenterata, Turb = Turbellaria, Olig = Oligochaeta, Hiru = Hirudinea, Ostr = Ostracoda, Amph = Amphipoda, Zoop = Cladocera and Copepoda, Acar = Acari, Plec = Plecoptera, Dipt = Diptera, Pele = Pelecypoda, Gast = Gastropoda.

[b] Because they were combined, four samples from 180-250 m were excluded.

[c] Only *Hyallela azteca* at 5-10 and 15-30 m and only *Stygobromus* spp. at greater depths.

[d] Includes both Chironomidae and Ceratopogonidae.

Appendix 2. Mean estimated number of bottom invertebrates per $m^2$ in Lake Tahoe, 1963 (standard deviations are in parentheses).[a]

| Depth range (m) | Samples | Coel | Turb | Nema | Olig | Hiru | Clad | Ostr | Amph[b] | Cope |
|---|---|---|---|---|---|---|---|---|---|---|
| 1-2 | 33 | 1 (8) | 6 (19) | 0 | 568 (739) | 0 | 247 (576) | 77 (160) | 21 (53) | 72 (124) |
| 5-10 | 48 | 1 (6) | 44 (86) | 3 (11) | 1600 (866) | 19 (89) | 187 (286) | 136 (209) | 172 (399) | 52 (82) |
| 15-30 | 48 | 0 | 56 (91) | 5 (19) | 1973 (776) | 7 (26) | 275 (472) | 414 (492) | 34 (89) | 30 (47) |
| 30-50 | 12 | 29 (70) | 269 (285) | 4 (12) | 2590 (1821) | 29 (76) | 244 (301) | 847 (1256) | 4 (12) | 54 (49) |
| 60-90 | 48 | 10 (36) | 195 (264) | 8 (25) | 2015 (961) | 3 (11) | 38 (59) | 1266 (1071) | 250 (494) | 36 (79) |
| 100-110 | 11 | 35 (117) | 364 (288) | 0 | 1198 (665) | 0 | 16 (22) | 313 (331) | 693 (620) | 70 (95) |
| 120-150 | 48 | 0 | 133 (157) | 14 (39) | 518 (410) | 0 | 5 (17) | 183 (270) | 458 (585) | 12 (29) |
| 225-300 | 9 | 0 | 91 (100) | 8 (19) | 846 (646) | 0 | 2 (6) | 128 (129) | 2198 (1717) | 11 (17) |
| 450-500 | 10 | 0 | 199 (197) | 6 (13) | 854 (522) | 0 | 2 (6) | 21 (29) | 710 (531) | 6 (9) |
| Total | 267 | | | | | | | | | |

[a] Coel = Coelenterata, Turb = Turbellaria, Nema = Nematoda, Olig = Oligochaeta, Hiru = Hirudinea, Clad = Cladocera, Ostr = Ostracoda, Amph = Amphipoda, Cope = Copepoda. Does not include one coleopteran larva collected at 482 m.

[b] Only *Hyallela azteca* at 1-2, 5-10, and 15-30 m and only *Stygobromus* spp. at greater depths.

Appendix 2. Continued.[c]

| Depth range (m) | Samples | Acar | Plec | Ephe | Tric | Chir | Cera | Pele | Gast |
|---|---|---|---|---|---|---|---|---|---|
| 1-2 | 33 | 60 (255) | 1 (8) | 31 88) | 0 | 611 (932) | 81 (181) | 4 (13) | 4 (17) |
| 5-10 | 48 | 31 (57) | 0 | 4 (15) | 4 (17) | 331 (366) | 15 (57) | 8 (28) | 13 (45) |
| 15-30 | 48 | 27 (53) | 1 (6) | 0 | 0 | 449 (621) | 4 (15) | 11 (26) | 20 (58) |
| 30-50 | 12 | 32 (58) | 0 | 0 | 0 | 169 (170) | 0 | 18 (43) | 40 (79) |
| 60-90 | 48 | 85 (190) | 80 (151) | 0 | 2 (9) | 281 (400) | 0 | 50 (92) | 51 (96) |
| 100-110 | 11 | 31 (51) | 20 (40) | 0 | 0 | 145 (171) | 4 (13) | 4 (13) | 16 (40) |
| 120-150 | 48 | 4 (12) | 2 (9) | 0 | 0 | 127 (215) | 0 | 3 (11) | 0 |
| 225-300 | 9 | 2 (6) | 2 (6) | 0 | 0 | 15 (13) | 0 | 0 | 0 |
| 450-500 | 10 | 0 | 0 | 0 | 0 | 31 (36) | 0 | 0 | 0 |
| Total | 267 | | | | | | | | |

[c] Acar = Acari, Plec = Plecoptera, Ephe = Ephemeroptera, Tric = Trichoptera, Chir = Chironomidae, Cera = Ceratopogonidae, Pele = Pelecypoda, Gast = Gastropoda.

Appendix 3. Percentage frequency of occurrence of bottom invertebrates in Lake Tahoe Ekman grab samples, 1962[a].

| Depth range (m) | Samples[b] | Coel | Turb | Olig | Hiru | Ostr | Amph[c] | Zoop | Acar | Plec | Dipt[d] | Pele | Gast |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 5-10 | 31 | - | 29.0 | 100.0 | - | 51.6 | 38.7 | 41.9 | 22.6 | 3.2 | 87.1 | 16.1 | 19.4 |
| 15-30 | 29 | - | 37.9 | 100.0 | 17.2 | 72.4 | 20.7 | 58.6 | 37.9 | 6.9 | 96.6 | 27.6 | 17.2 |
| 60-90 | 32 | 12.5 | 43.8 | 96.9 | 9.4 | 78.1 | 31.2 | 37.5 | 25.0 | 37.5 | 71.9 | 18.8 | 34.4 |
| 120-150 | 23 | - | 34.8 | 87.0 | - | 60.9 | 73.9 | 34.8 | 8.7 | 21.7 | 34.8 | 4.3 | 4.3 |
| 350-400 | 2 | - | 50.0 | 100.0 | - | 100.0 | 100.0 | 50.0 | - | - | 50.0 | - | - |
| 450-500 | 3 | - | 100.0 | 100.0 | - | 33.3 | 100.0 | 33.3 | - | - | - | - | - |
| Total | 120 | 3.3 | 38.3 | 96.7 | 6.7 | 65.8 | 41.7 | 43.3 | 23.3 | 16.7 | 72.5 | 16.7 | 19.2 |

[a] Coel = Coelenterata, Turb = Turbellaria, Olig = Oligochaeta, Hiru = Hirudinea, Ostr = Ostracoda, Amph = Amphipoda, Zoop = Cladocera and Copepoda, Acar = Acari, Plec = Plecoptera, Dipt = Diptera, Pele = Pelecypoda, Gast = Gastropoda.

[b] Because they were combined, four samples from 180-250 m were excluded.

[c] Only *Hyallela azteca* at 5-10 and 15-30 m and only *Stygobromus* spp. at greater depths.

[d] Includes both Chironomidae and Ceratopogonidae.

Appendix 4. Percentage frequency of occurrence of bottom invertebrates in Lake Tahoe Ekman grab samples, 1963[a].

| Depth range (m) | Samples | Coel | Turb | Nema | Olig | Hiru | Clad | Ostr | Amph[b] | Cope |
|---|---|---|---|---|---|---|---|---|---|---|
| 1-2 | 33 | 3.0 | 12.1 | - | 93.9 | - | 42.4 | 39.4 | 21.2 | 48.5 |
| 5-10 | 48 | 2.1 | 37.5 | 6.2 | 100.0 | 12.5 | 60.4 | 60.4 | 43.8 | 45.8 |
| 15-30 | 48 | - | 47.9 | 8.3 | 100.0 | 8.3 | 75.0 | 93.8 | 29.2 | 41.7 |
| 30-50 | 12 | 16.7 | 91.7 | 8.3 | 100.0 | 16.7 | 83.3 | 91.7 | 8.3 | 75.0 |
| 60-90 | 48 | 10.4 | 72.9 | 12.5 | 100.0 | 6.2 | 43.8 | 95.8 | 45.8 | 27.1 |
| 100-110 | 11 | 9.1 | 100.0 | - | 100.0 | - | 36.4 | 81.8 | 100.0 | 45.5 |
| 120-150 | 48 | - | 70.8 | 16.7 | 82.3 | - | 10.4 | 72.9 | 77.1 | 16.7 |
| 225-300 | 9 | - | 66.7 | 22.2 | 100.0 | - | 11.0 | 100.0 | 100.0 | 33.3 |
| 450-500 | 10 | - | 70.0 | 20.0 | 90.0 | - | 10.0 | 60.0 | 100.0 | 30.0 |
| Total | 267 | 3.7 | 55.8 | 9.7 | 95.9 | 5.6 | 45.3 | 76.0 | 49.4 | 37.1 |

| Depth range (m) | Samples | Acar | Plec | Ephe | Tric | Chir | Cera | Pele | Gast |
|---|---|---|---|---|---|---|---|---|---|
| 1-2 | 33 | 24.2 | 3.0 | 24.2 | - | 81.8 | 27.3 | 9.1 | 6.1 |
| 5-10 | 48 | 35.4 | - | 6.2 | 4.2 | 81.2 | 10.4 | 12.5 | 12.5 |
| 15-30 | 48 | 35.4 | 2.1 | - | - | 95.8 | 6.2 | 18.8 | 16.7 |
| 30-50 | 12 | 33.3 | - | - | - | 66.7 | - | 16.7 | 33.3 |
| 60-90 | 48 | 31.2 | 39.6 | - | 4.2 | 81.2 | - | 39.6 | 33.3 |
| 100-110 | 11 | 45.5 | 27.3 | - | - | 81.8 | 9.1 | 9.1 | 18.2 |
| 120-150 | 48 | 8.3 | 4.2 | - | - | 64.6 | - | 6.2 | - |
| 225-300 | 9 | 11.1 | 11.1 | - | - | 66.7 | - | - | - |
| 450-500 | 10 | - | - | - | - | 60.0 | - | - | - |
| Total | 267 | 26.6 | 10.1 | 4.1 | 1.5 | 79.0 | 6.7 | 16.1 | 14.2 |

[a] Coel = Coelenterata, Turb = Turbellaria, Nema = Nematoda, Olig = Oligochaeta, Hiru = Hirudinea, Clad = Cladocera, Ostr = Ostracoda, Amph = Amphipoda, Cope = Copepoda, Acar = Acari, Plec = Plecoptera, Ephe = Ephemeroptera, Tric = Trichoptera, Chir = Chironomidae, Cera = Ceratopogonidae, Pele = Pelecypoda, Gast = Gastropoda.

[b] Only *Hyallela azteca* at 1-2, 5-10, and 15-30 m and only *Stygobromus* spp. at greater depths.

Appendix 5. Mean estimated densities (number per $m^2$) of Lake Tahoe macrobenthos by locality, 1963.

| | | Depth range (no. samples) | | | | |
|---|---|---|---|---|---|---|
| | | 1-2 (33) | 5-10 (48) | 15-30 (48) | 60-90 (48) | 120-150 (48) |
| Tubellaria | Cave Rock | 0 | 11 | 54 | 276 | 111 |
| | South Tahoe | 27 | 136 | 133 | 283 | 140 |
| | McKinney Bay | 0 | 25 | 22 | 118 | 143 |
| | Crystal Bay | 0 | 3 | 14 | 104 | 136 |
| Oligochaeta | Cave Rock | 198 | 764 | 2,038 | 2,027 | 592 |
| | South Tahoe | 999 | 1,851 | 1,647 | 2,242 | 369 |
| | McKinney Bay | 913 | 2,551 | 1,902 | 1,894 | 434 |
| | Crystal Bay | 113 | 1,224 | 2,300 | 1,894 | 678 |
| Ostracoda | Cave Rock | 5 | 29 | 337 | 1,927 | 104 |
| | South Tahoe | 285 | 172 | 177 | 1,109 | 298 |
| | McKinney Bay | 24 | 316 | 449 | 1,044 | 100 |
| | Crystal Bay | 0 | 25 | 682 | 987 | 229 |
| Amphipoda | Cave Rock | 11 | 11 | 36 | 556 | 642 |
| | South Tahoe | 70 | 266 | 75 | 434 | 194 |
| | McKinney Bay | 0 | 412 | 11 | 11 | 86 |
| | Crystal Bay | 5 | 0 | 14 | 0 | 911 |
| Cladocera | Cave Rock | 16 | 86 | 456 | 40 | 11 |
| | South Tahoe | 522 | 219 | 143 | 40 | 3 |
| | McKinney Bay | 416 | 266 | 240 | 36 | 7 |
| | Crystal Bay | 11 | 176 | 262 | 36 | 0 |
| Diptera | Cave Rock | 183 | 352 | 416 | 208 | 136 |
| | South Tahoe | 410 | 384 | 212 | 108 | 72 |
| | McKinney Bay | 1,652 | 427 | 578 | 93 | 54 |
| | Crystal Bay | 393 | 215 | 570 | 700 | 244 |
| Others | Cave Rock | 32 | 67 | 63 | 595 | 32 |
| | South Tahoe | 264 | 307 | 228 | 528 | 31 |
| | McKinney Bay | 377 | 97 | 71 | 132 | 31 |
| | Crystal Bay | 27 | 69 | 73 | 60 | 42 |
| Total | Cave Rock | 445 | 1,320 | 3,400 | 5,629 | 1,628 |
| | South Tahoe | 2,577 | 3,335 | 2,615 | 4,744 | 1,107 |
| | McKinney Bay | 3,382 | 4,094 | 3,273 | 3,328 | 855 |
| | Crystal Bay | 549 | 1,712 | 3,915 | 3,781 | 2,240 |

CALIFORNIA FISH AND GAME
*California Fish and Game* 82(1):42-47 1996

# USE OF FOOD ITEMS BY SEX AND AGE CLASSES OF COYOTES

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**Food use by coyotes, *Canis latrans*, was compared between sexes and among age classes at the Naval Petroleum Reserves in California. Frequency of occurrence of items did not differ significantly between males and females. Although leporids were the food most frequently used by all age classes, item use differed significantly between pups (<1 yr), yearlings (1 yr), and adults (>1 yr), probably because of differential use of secondary items. Variation in food use among age classes could potentially bias results of coyote diet studies.**

## INTRODUCTION

Coyotes, *Canis latrans*, are ecologically important in California due to their widespread distribution, abundance, and potential effects on prey populations and livestock. Coyote foraging patterns have been extensively studied and several investigations have been conducted in California (Ferrel et al. 1953, Hawthorne 1972, Bowyer et al. 1983, Bowyer 1987, Cypher et al. 1994). However, diet variation among sexes and age classes was rarely addressed. Such variation, if significant, potentially could bias foraging studies. As part of an investigation of coyote diets in the southern San Joaquin Valley, California (Cypher et al. 1994), food use was compared between sexes and among three age classes.

## STUDY AREA

The investigation was conducted at the Naval Petroleum Reserves in California (NPRC), 42 km southwest of Bakersfield in western Kern County, California (119°W 35°N). The Naval Petroleum Reserves in California includes approximately 31,000 ha and the primary land use is the production of petroleum. The Naval Petroleum Reserves in California encompasses a series of east-west anticlinal ridges that are surrounded by gently sloping alluvial plains. Elevations range from 88 to 473 m (Woodring et al. 1932). The climate is characterized by hot (29°C), dry summers and cool (9°C) winters with frequent fog; annual precipitation averages approximately 12.5 cm and occurs primarily as rain between November and April

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(National Oceanic and Atmospheric Administration[4] 1992).

The vegetation association has been classified variously as Lower Sonoran Grassland (Twisselman 1967), Valley Grassland (Heady 1977), or Valley Saltbush Scrub (Holland[5] 1986). Herbaceous vegetation consists primarily of naturalized annual grasses and forbs; common shrubs include desert saltbush, *Atriplex polycarpa*; bladderpod, *Isomeris arborea*; and cheesebush, *Hymenoclea salsola*. Common potential prey for coyotes include black-tailed jackrabbit, *Lepus californicus*; desert cottontail, *Sylvilagus audubonii*; San Joaquin kangaroo rat, *Dipodomys nitratoides*; and Heermann's kangaroo rat, *D. heermanni*. Domestic sheep are grazed on approximately one-half of NPRC each spring and potentially are available to coyotes either as prey or carrion.

## METHODS

Diet of coyotes was determined by stomach content analysis. From 1985 to 1990, 591 coyotes were removed from NPRC in an effort to reduce predation on the endangered San Joaquin kit fox, *Vulpes macrotis mutica* (Cypher and Scrivner 1992). Stomachs were collected from some carcasses and frozen. Stomachs were later thawed, and contents were rinsed in a strainer and spread on a tray for identification. All items occurring in stomachs were identified. Many items were entirely or partially intact, permitting easy identification. For disassociated items, mammalian remains were identified by comparing teeth and skull fragments with reference specimens. Unknown hair was identified using macroscopic (e.g., length, texture, color, and banding patterns) and microscopic (e.g., cuticular scale and medulla patterns) characteristics (Mayer 1952, Moore et al. 1974). Diagnostic parts of birds (skulls, bills, feet, and feathers), reptiles (skulls and scales), and insects (exoskeletons) were collected for comparison to known specimens. Fruit seeds were identified according to Young and Young (1992).

Frequency of occurrence of items in coyote stomachs was determined for each age class and sex. Age classes were pups (<1 yr), yearlings (1 yr), and adults (>1 yr); ages were determined by cementum annuli analysis (Matson's Laboratory, Milltown, Montana 59851). Age information was available for 215 coyotes. Samples were pooled across years. We used chi-square analysis to compare food item occurrences among age classes and between sexes. For statistical analyses, items were grouped as leporids, rodents, livestock, birds, insects, and other items. Results were considered significant if $P < 0.05$.

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[4] National Oceanic and Atmospheric Administration. 1992. Local climatological data, 1992: Annual summary with comparative data, Bakersfield, California. National Oceanic and Atmospheric Administration Report No. ISSN 0198-0696, Asheville, North Carolina, USA.

[5] Holland, R.F. 1986. Preliminary descriptions of the terrestrial natural communities of California. California Department of Fish and Game, Sacramento, California, USA.

## RESULTS

Coyotes at the NPRC consumed a wide variety of food. The diet was dominated by leporids (66.5%), which consisted primarily of black-tailed jackrabbit and infrequent desert cottontail; however, identification to species was only occasionally possible. The most commonly encountered rodents were kangaroo rat (Heermann's and San Joaquin, 8.7%); pocket gopher, *Thomomys bottae* (5.4%); and California ground squirrel, *Spermophilus beecheyi* (2.1%). Other rodents included San Joaquin pocket mouse, *Perognathus inornatus* (0.4%); San Joaquin antelope squirrel, *Ammospermophilus nelsoni* (0.8%); deer mouse, *Peromyscus maniculatus* (0.4%); and house mouse, *Mus musculus* (0.4%). Livestock occurring in stomachs included sheep (7.9%), pig (1.2%), and cow or goat (9.1%); livestock likely was consumed as carrion (Cypher et al. 1994). Identifiable bird remains included California quail, *Lophortyx californicus* (1.7%); roadrunner, *Geococcyx californianus* (0.4%); western meadowlark, *Sturnella neglecta* (0.4%); and eggs (0.8%). Insects were primarily beetles (mostly *Eleodes*, 8.3%), Jerusalem cricket (Gryllacrididae, 7.4%), and grasshopper (Acrididae, 2.5%), but also included cockroach (Blattidae, 0.8%), wasp (Vespidae, 0.8%), and dragonfly (Odonata, 0.8%). Other items included mule deer, *Odocoileus hemionus* (0.8%); long-tailed weasel, *Mustela frenata* (0.4%); coyote (2.5%); gopher snake, *Pituophis melanoleucus* (0.8%); side-blotched lizard, *Uta stansburiana* (0.8%); skink, *Eumeces* (0.4%); grape, *Vitis* (0.4%); pear or apple, *Malus* (0.4%); peach, *Prunus persica* (1.2%); mulberry, *Morus* (0.4%); and refuse (paper, cellophane, rubber, and cloth, 5.8%). No San Joaquin kit fox remains were found in coyote stomachs.

Frequency of occurrence of food items consumed by coyotes did not differ between males and females (Table 1) for adults ($\chi^2 = 3.39$, df = 5, $P = 0.64$), yearlings ($\chi^2 = 4.65$, df = 5, $P = 0.46$), or pups ($\chi^2 = 7.10$, df = 5, $P = 0.21$), but did differ among

Table 1. Comparison of food item use between male and female coyotes at the Naval Petroleum Reserves in California, 1985-90.

| | Frequency of Occurrence (%) | | | | | |
|---|---|---|---|---|---|---|
| | Adults[a] | | Yearlings[b] | | Pups | |
| Item | Male (n=52) | Female (n=33) | Male (n=33) | Female (n=24) | Male (n=41) | Female (n=26) |
| Leporid | 75.0 | 78.8 | 72.7 | 41.7 | 68.3 | 53.8 |
| Rodent | 11.5 | 24.2 | 24.2 | 29.2 | 12.2 | 26.9 |
| Livestock | 11.5 | 18.2 | 21.2 | 33.3 | 9.8 | 23.1 |
| Bird | 11.5 | 15.2 | 21.2 | 16.7 | 14.6 | 15.4 |
| Insect | 1.9 | 9.1 | 9.1 | 16.7 | 43.9 | 46.2 |
| Other | 11.5 | 21.2 | 15.2 | 25.0 | 31.7 | 11.5 |

[a] Four additional adults were sampled, but sex was not recorded. They appear in Table 2, but not here.

[b] Two additional yearlings were sampled, but sex was not recorded. They appear in Table 2, but not here.

coyote age classes ($\chi^2 = 37.15$, df = 10, $P < 0.01$; Table 2). Proportional occurrence of items differed significantly between pups and yearlings ($\chi^2 = 12.54$, df = 5, $P = 0.03$) and between pups and adults ($\chi^2 = 25.43$, df = 5, $P < 0.01$), but not between yearlings and adults ($\chi^2 = 10.21$, df = 5, $P = 0.07$). Since leporid was the most frequently occurring item for all age classes, dietary variations among age classes were the result of differential use of other items. The most frequently occurring items other than leporid included rodent for adults, livestock and rodent for yearlings, and insect for pups.

## DISCUSSION

Although coyotes are sexually dimorphic (Bekoff 1977), food item use by males and females at NPRC was similar. Sexual dimorphism apparently is not sufficient to optimize sex-specific foraging efficiency through differential food item use, as has been observed in the fisher, *Martes pennanti* (Kuehn 1989).

Differential use of foods among coyote age classes may have been a function of age-specific foraging experience. Yearlings are less experienced than adults. Livestock, particularly carrion, and birds may have been more easily obtained by yearlings. Pups are less experienced hunters than either yearlings or adults, and they frequently consumed insects. Insects constitute easy prey for coyote pups (Wells and Bekoff 1982) and high use of insects by pups also has been observed in northeastern California (Hawthorne 1972). Differential food use may reduce resource competition among age classes.

Differential use of foods by coyote age classes potentially could bias the results of coyote diet investigations. For example, a disproportionate number of samples from a particular age class could result in data that were less representative of actual coyote diets in a given area. Unfortunately, correcting for such bias may be difficult because the age structure of a given coyote population usually is unknown and the age of the animal from which a food habit sample is collected (particularly for fecal samples) also usually is unknown. However, data on diets will probably not be significantly biased so long as a particular age class is not overrepresented within the samples.

Table 2. Comparison of food item use among coyote age classes at the Naval Petroleum Reserves in California, 1985-90.

| | Frequency of Occurrence (%) | | |
|---|---|---|---|
| Item | Adults (n=89) | Yearlings (n=59) | Pups (n=67) |
| Leporid | 76.4 | 57.6 | 62.7 |
| Rodent | 18.0 | 27.1 | 19.4 |
| Livestock | 13.5 | 27.1 | 17.9 |
| Bird | 13.5 | 20.3 | 14.9 |
| Insect | 4.5 | 11.9 | 41.8 |
| Other | 14.6 | 25.4 | 26.9 |

Also of interest was the absence of kit fox remains in coyote stomachs. Coyotes have been identified as a significant source of mortality for kit foxes at NPRC (Cypher and Scrivner 1992) and at other locations (Disney and Spiegel 1992, Ralls and White 1995). Although Ralls and White (1995) reported that more than half of the foxes killed by coyotes had been fed upon, coyotes rarely consumed fox carcasses at NPRC (Berry et al.[6] 1987) or the nearby Lokern Natural Area (Disney and Spiegel 1992). Thus, much of this mortality may constitute interference competition by coyotes instead of classical predation. Sperry (1941) reported kit fox remains in only two of 8,357 coyote stomachs collected in New Mexico and Texas.

## ACKNOWLEDGMENTS

This research was sponsored by the U.S. Department of Energy (DOE), Naval Petroleum Reserves in California, and Chevron U.S.A., Inc. under contract number DE-AC08-93NV11265 with the DOE Nevada Operations Office. We thank the many EG&G Energy Measurements, Inc. staff members who helped collect coyote stomachs. P. Butchko, J. Bennett, and R. Moschetti of the United States Department of Agriculture, Division of Animal Damage Control, conducted the coyote control program at NPRC and provided the carcasses from which stomachs were collected. We thank T. Kato, G. Warrick, K. Ostler, and two anonymous reviewers for constructive criticism on the manuscript.

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Received: 28 August 1995
Accepted: 19 December 1995

CALIFORNIA FISH AND GAME
*California Fish and Game* 82(1):48-53 1996

# NOTES ON THE OCCURRENCE AND DEPTH DISTRIBUTION OF THE BAT RAY IN THE SOUTHERN CALIFORNIA BIGHT, WITH COMMENTS ON THE EFFECT OF TRAWL SIZE ON ESTIMATES OF ABUNDANCE

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The bat ray, *Myliobatis californica*, is a relatively large benthic predator found in shallow inshore waters from Oregon to the Gulf of California (Miller and Lea 1972). It is commonly associated with bays and estuaries, where most observations and collections for life history studies have occurred (Talent 1982, 1985; Martin and Cailliet 1988a, 1988b; Hopkins 1994).

Bat rays, which feed primarily on benthic invertebrates, excavate feeding pits which can exceed 30 cm across and 30 cm deep (Talent 1982, Van Blaricom 1982 and pers. comm.). Excavation of these pits is believed to occur through forceful jetting of water from the mouth, gills, or both (Gregory et al. 1979). Bat ray feeding behavior can cause considerable localized sediment disturbance and may influence invertebrate and plant community structure (Orth 1975, 1976; Van Blaricom 1982; Thrush et al. 1991).

The distribution and seasonal movements of bat rays are not well known; however, they are most abundant in Elkhorn Slough and Tomales Bay during spring through fall and rare or absent during winter (Talent 1985, Hopkins[1] 1993). This time period of high inshore abundance overlaps with the spring and summer spawning and breeding season (Martin and Cailliet 1988a). Bat rays apparently move out of shallow bays and estuaries during the winter months to avoid temperature and salinity extremes (Hopkins[1] 1993).

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[1] Hopkins, T.E. 1993. The physiological ecology of bat rays, *Myliobatis californica*, in Tomales Bay, California. Ph.D. Dissertation, University of California, Davis, California, USA.

Eschmeyer et al. (1983) list the depth range for bat rays as from the intertidal to 46 m, although their distribution has not been thoroughly investigated. The standard scientific method for sampling nearshore, soft-bottom-associated fishes has been with relatively small otter trawls (Mearns and Stubbs[2] 1974, Mearns and Allen[3] 1978). Recent surveys employing a larger trawl indicate that bat rays occur in deeper water than listed in published literature and that their population may be undersampled with the traditional small scientific trawls. Our paper is intended to update current information on the occurrence and distribution of bat rays in the Southern California Bight and to illustrate catch differences associated with two gear types. The data are derived from unpublished trawl records from the California Department of Fish and Game (CDFG) and the Vantuna Research Group of Occidental College (VRG).

A series of 147 benthic trawls (Fig. 1) was conducted by the CDFG to survey soft-bottom habitats throughout the Southern California Bight from 14 February to 18 March 1994. Trawling depths ranged from 9 to 110 m; duration was 20 min; and the net used was a 400-mesh, commercial-type Eastern Trawl with dimensions of 15 m wide by 1.5 m high, a 10.2-cm mesh body, and a 8.9-cm mesh cod end. The occurrence and number of bat rays captured by these trawls are compared with similar values for otter trawls fished by the VRG from 1973 to 1993, covering approximately the same geographical area at depths from 6 to 92 m (Fig. 2). These trawls were standard semi-balloon 4.9- or 7.6-m otter trawls with 3.8-cm body mesh and 1.3-cm cod-end mesh. They are about one-third and one-half as large as the net used by CDFG. Duration of trawls varied from 5 to 20 min. In addition to numerical abundance of bat rays collected, the VRG data also include disk width (DW) measurements (from wing tip to wing tip) for most samples.

The area swept by CDFG and VRG trawls was estimated by multiplying the length of each haul (estimated from vessel speed and tests with a time-depth recorder) by recognized estimates of the width of the trawl mouth opening. These calculations allowed standardization of data as catch per hectare. Although these trawls are designed to sample organisms on or near the bottom, individuals may be collected in the water column during net deployment and retrieval. Bat rays in these studies were assumed to have been collected at the trawl fishing depths; however, it should be noted that single individuals and a large aggregation of bat rays have been observed in the water column in coastal areas of southern California (Odenweller 1975; J.S. Stephens, pers. obs.).

The total number of bat rays collected in the 147 CDFG trawls was 919, a mean catch per trawl of 6.3 rays (SD = 20.9). Bat rays occurred in 38.8% of the trawls at a density of 3.09/ha. Catch and latitude were not significantly correlated within the

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[2] Mearns, A.J. and H.H. Stubbs. 1974. Comparison of otter trawls used in southern California coastal surveys. Southern California Coastal Water Research Project, Westminster, California, USA. SCCWRP-TM213.

[3] Mearns, A.J. and J. Allen. 1978. Use of small trawls in coastal biological surveys. United States Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon, USA. EPA-600/3-78-083.

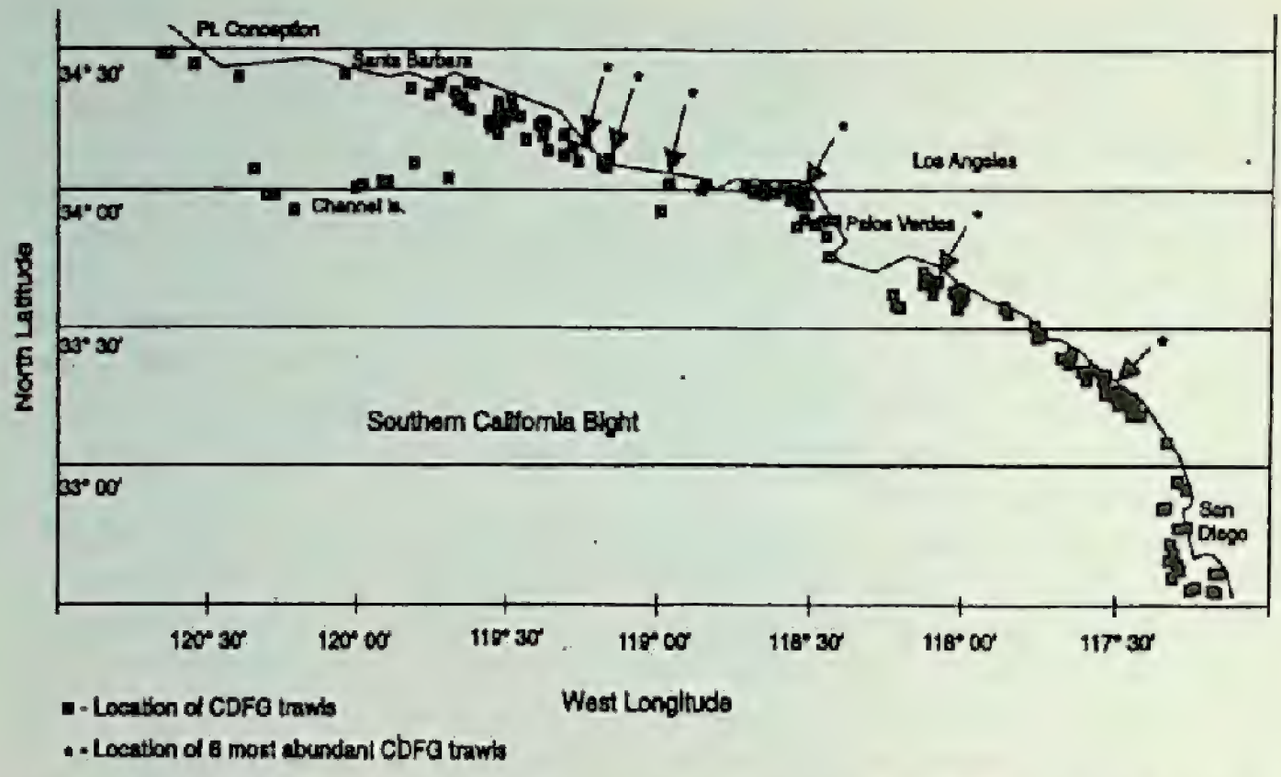


Figure 1. Location of California Department of Fish and Game trawls in the Southern California Bight in 1994, N = 147.

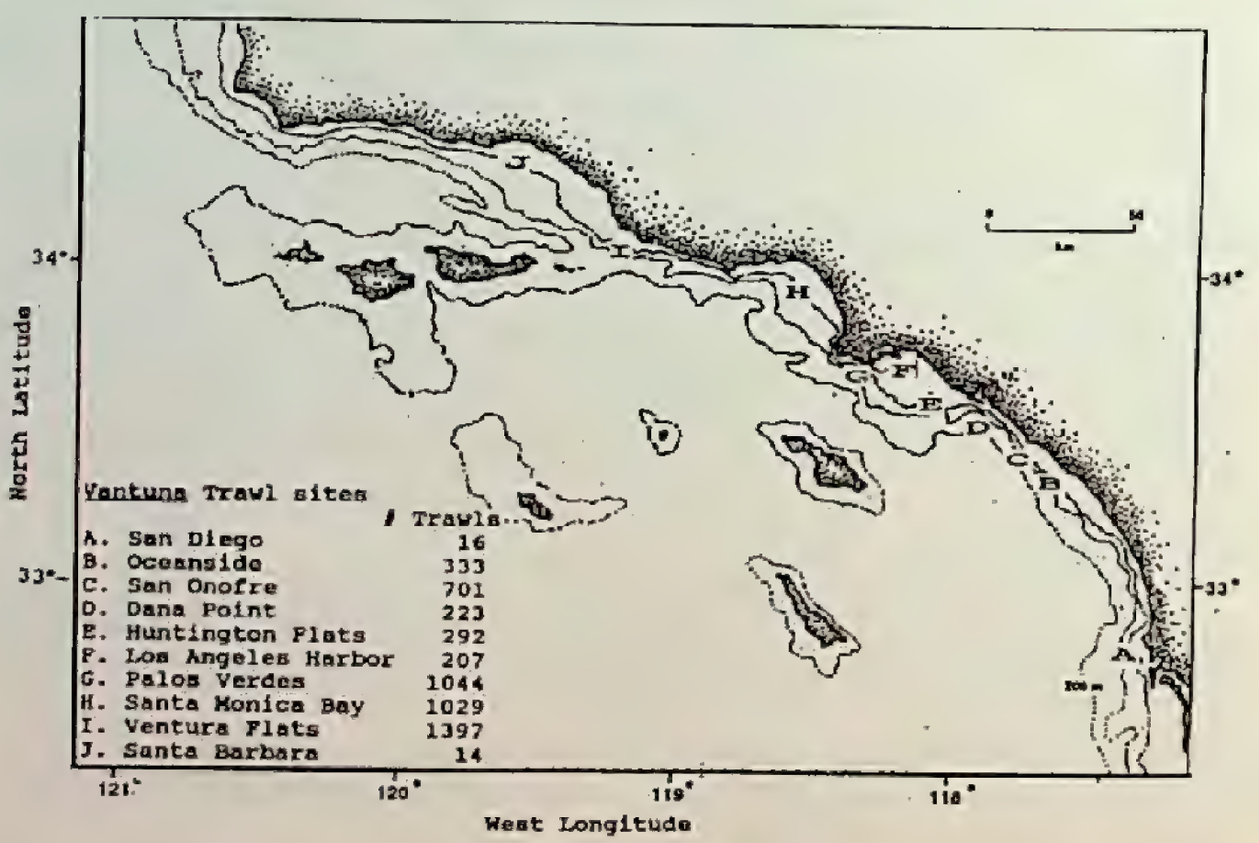


Figure 2. Location and distribution of Vantuna Research Group trawls in the Southern California Bight from 1972 to 93, N = 5,256.

bight (r = 0.01, $P = 0.89$); however, the largest hauls occurred at the north end of Santa Monica Bay (168 rays/trawl), off Huntington Beach (129 rays/trawl), near the Pt. Mugu/Pt. Dume area (76, 73, and 72 rays/trawl), and near Oceanside (50 rays/trawl).

Depth of trawl and catch of bat rays were significantly correlated, as catch declined with increased water depth (r = 0.72, $P < 0.02$, Fig. 3). The largest hauls of bat rays mentioned above were all collected from water ≤20 m deep. Although more bat rays were caught in shallower water, they were collected as deep as 108 m. This is considerably deeper than the 46 m listed as the depth limit for bat rays (Miller and Lea 1972, Eschmeyer et al. 1983).

A total of 303 bat rays was collected in 5,674 VRG trawls. This yields a mean catch of 0.05 rays/trawl (SD = 0.23), but trawl duration varied. The frequency of occurrence in VRG trawls was 5.2% at a density of 0.14 rays/ha. Bat rays were collected as deep as 92 m and showed a depth distribution similar to the CDFG data, in which abundance decreased as depth increased (r = 0.79, $P < 0.01$, Fig. 3). Mean size was 433.6 mm DW (SD = 142.2 mm), with a range of 175-999 mm DW[4]. The size frequency distribution was skewed towards smaller individuals, as 90% of

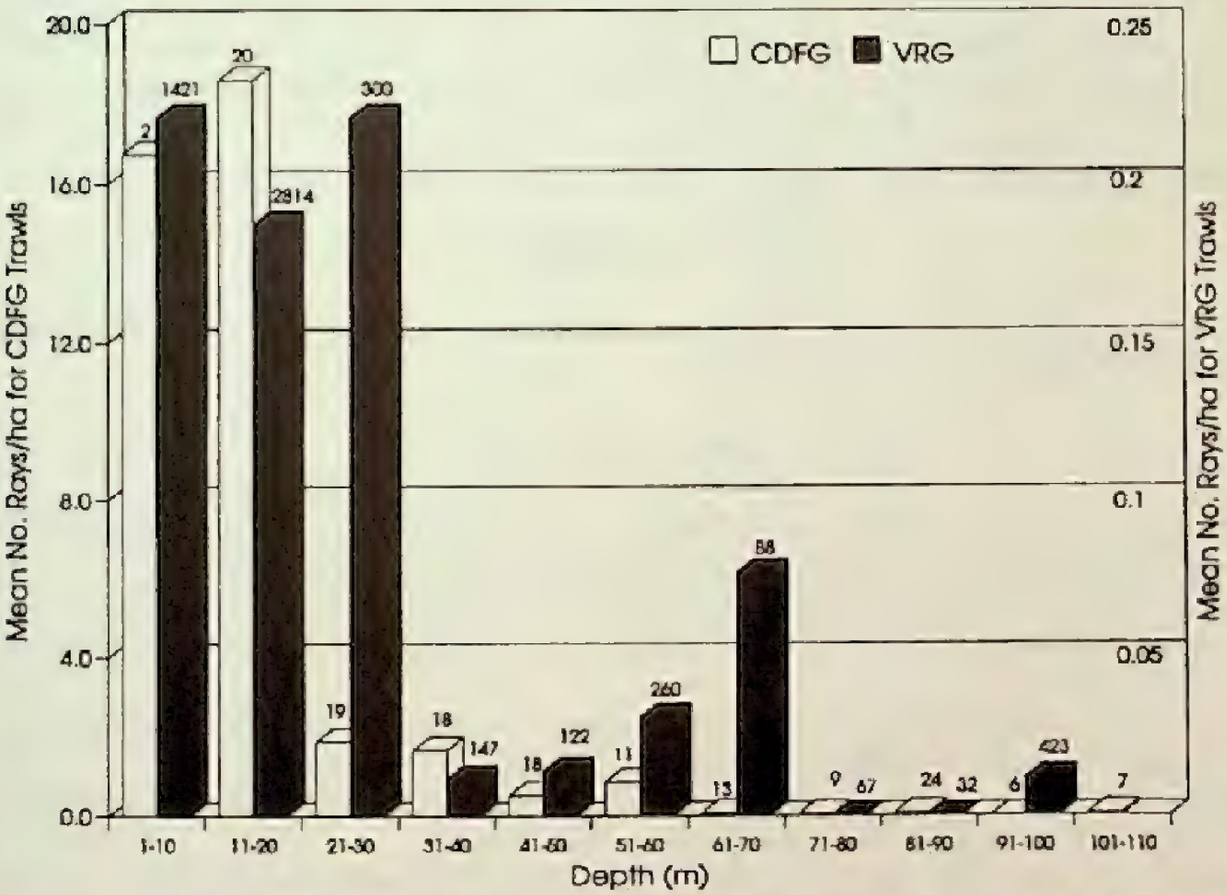


Figure 3. Depth stratified density of bat rays collected in the Southern California Bight by California Department of Fish and Game (1994) and Vantuna Research Group (1972-93) trawls. Numbers above each column indicate the number of trawls at that depth stratum. Separate y-axis scales are used for the two data sets to allow visualization of both on one figure.

[4]The highest usable size value in the VRG data base was 999; therefore, the actual maximum size could be larger. However, only one individual had a value of 999.

measured bat rays were <630 mm DW. Trawl depth and size were not significantly correlated ($r = 0.09$, $P > 0.10$), although the largest fish were collected from shallow water.

This comparison of CDFG and VRG data, although during different time periods, indicates a considerably higher occurrence and density of bat rays when using the larger CDFG trawl. An examination of VRG diver transect data from Palos Verdes Point and King Harbor that bridges the two sampling periods (1974-1995) does not suggest an increase in abundance of bat rays in 1994. While Fig. 1 shows a similar density versus depth pattern, the density of bat rays in CDFG trawls averages >22 times higher than the density in VRG trawls. This suggests that bat rays may be undersampled due to net avoidance when using the smaller, standard scientific otter trawls. Both the CDFG and VRG data indicate bat rays are found in deeper water than previous literature suggested. Further examination of the VRG data indicates that catches during the summer were less than one-half that of other seasons. These data support the theory that bat rays move into shallow bays and inlets not sampled in the VRG samples during the summer for spawning and breeding (Martin and Cailliet 1988a, Talent 1985). However, the VRG data also showed that some bat rays were present in water >50 m deep during all seasons of the year. Studies of other large, mobile, benthic fishes may benefit from sampling with the gear employed by CDFG. Knowledge of the depth range and abundance of bat rays should assist life history studies and research on sediment disturbance and bioturbation.

## ACKNOWLEDGMENTS

We thank M. Helvey for helpful comments on the manuscript and crews of the *R/V MAKO* and the *R/V VANTUNA*.

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Received: 10 January 1995
Accepted: 14 August 1995

*California Fish and Game* 82(1):54-58 1996

# COMPARISON OF JUVENILE CHINOOK SALMON CATCHES IN A PUSHNET AND MIDWATER TRAWL

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Sampling for fishes with conventional towed gear, such as a midwater trawl, is often difficult or impossible in shallow embayments and behind structures, such as radial gates. A relatively new sampling gear, the pushnet, may be more suitable for these situations (Kriete and Loesch 1980; Vogel[2] 1987; W. Loudermilk, California Department of Fish and Game, pers. comm.).

A pushnet is a bow-mounted fixed-frame net pushed in front of a vessel to catch fish in the upper layer of the water column. It can be operated in shallow water, static or flowing water, or immediately in front of the discharge of a dam or similar water control structure. In spite of the apparent versatility of the pushnet, its efficiency relative to other gears has not been established.

My study is a limited test of the relative efficiency of a bow-mounted pushnet and a midwater trawl for capturing juvenile chinook salmon, *Oncorhynchus tshawytscha*. I compared catch density and fork length of chinook salmon caught in these two gears fished during daylight on 10 and 25 May 1990 in the Sacramento River near Courtland, California. Samples were of 10-min duration against the current along three equally-spaced transects across the width of the channel. All chinook salmon collected were counted and, when possible, at least 45 fish per sample were measured to the nearest millimeter fork length. At the time of sampling, tidal stage, water temperature, and water transparency (Secchi disc depth) also were measured. River flow data for each sampling date were obtained from the California Department of Water Resources.

The 7.2-m-long pushnet (Fig. 1a) was mounted on a 7-m skiff powered by a 5.7-liter inboard/outboard gasoline engine (Fig. 2). The net was attached with snaps to rings spaced every 30.5 cm along a rigid rectangular frame constructed of 5.1-cm diameter aluminum tubing. The pushnet frame was suspended over the bow from a 1.8-m by 2.4-m framework of 5.1-cm diameter aluminum tubing mounted on top of the gunwales (Fig. 2). The pushnet was raised and lowered by a 4.8-mm diameter stainless steel cable running from a cable bridle on the top of the net frame, through a pulley on the framework, to a 12-v electric winch mounted facing forward on an

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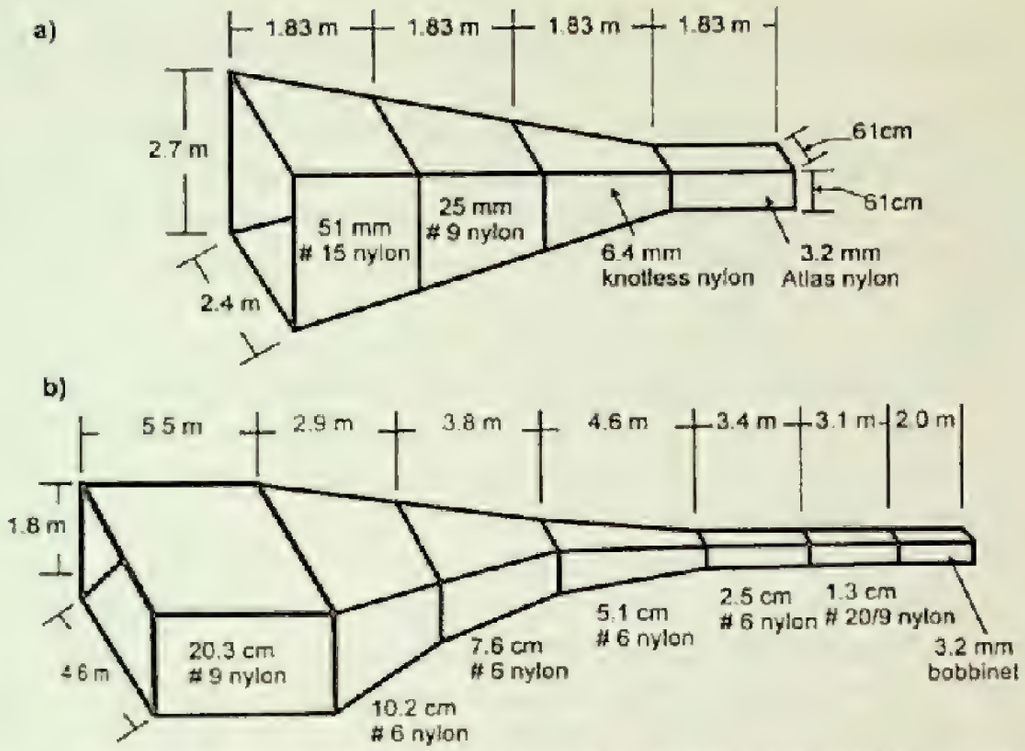


Figure 1. Design details of (a) the pushnet and (b) the midwater trawl used to compare catches of juvenile chinook salmon in the Sacramento River, May 1990. Mesh sizes are stretch mesh.

Figure 2. The pushnet vessel on a trailer with the pushnet frame and net in a forward position. The top of the frame is slightly above the vessel's waterline when in the correct position for fishing.

aluminum stand positioned just aft of amidships.

The midwater trawl (Fig. 1b) was towed behind a 7.0-m skiff powered by a 4.1-liter inboard/outboard gasoline engine. The net was attached via wings to the top and bottom doors, which were connected to a 30.5-m bridle of 4.8-mm diameter stainless steel cable. The net was set and retrieved by two 12-v electric winches

mounted facing rearward on square-tubing steel stands positioned just aft of amidships.

Catch densities were estimated by dividing chinook salmon catch by the water volume sampled. Water volume was estimated by multiplying the area of the net opening by the distance sampled, measured by a digital flowmeter suspended off the side of each skiff. Sampling speed was maintained as closely as possible to 3.2 km/h for both skiffs.

Catch density and mean fork length for the two gears were compared using ANOVA, after arc-sine transformation to normalize catch densities.

Catch densities of chinook salmon in the pushnet and midwater trawl were similar (Table 1). On 10 May 1990, mean density in seven pushnet samples (0.0269 fish/$m^3$) was not significantly different ($F = 0.02$, $P = 0.885$) than for six midwater trawl samples (0.0258 fish/$m^3$). Although density was much lower on 25 May, mean density in 12 pushnet samples (0.0009 fish/$m^3$) again was not significantly different ($F = 1.74$, $P = 0.200$) than for 12 midwater trawl samples (0.0015 fish/$m^3$).

Based on measuring almost 800 juvenile chinook salmon, both gears caught similar-sized fish (Fig. 3, Table 2). Mean fork length on 10 May of 345 chinook salmon caught in the pushnet (79.1 mm) was not significantly different ($F = 1.27$, $P = 0.283$) than for 300 fish collected in the midwater trawl (82.1 mm). On 25 May, 51 chinook salmon from the pushnet averaged 79.5 mm while 97 fish caught in the midwater trawl were 79.1 mm mean length; this difference also was not statistically significant ($F = 0.08$, $P = 0.785$).

On 10 May 1990, river flow measured at Freeport (17.7 km upstream of Courtland) was about 240 $m^3/s$. Water temperature was 20°C and water transparency was 125 cm. On 25 May 1990, river flow was approximately 370 $m^3/s$; water temperature was 17.8°C and water transparency measured 127 cm.

Testing relative efficiency of a bow-mounted pushnet and a midwater trawl for

Table 1. Chinook salmon catch statistics for pushnet and midwater trawl samples collected in the Sacramento River near Courtland, California, May 1990. Numbers in parentheses are standard deviations.

| Date/gear | Number of tows | Total catch | Mean volume sampled ($m^3$) | Mean catch density (no./$m^3$) | F | P |
|---|---|---|---|---|---|---|
| May 10 | | | | | | |
| Pushnet | 7 | 910 | 4931 (258) | 0.0269 (0.0151) | | |
| Midwater trawl | 6 | 793 | 5223 (417) | 0.0258 (0.0104) | 0.02 | 0.885 |
| May 25 | | | | | | |
| Pushnet | 12 | 53 | 4976 (762) | 0.0009 (0.0006) | | |
| Midwater trawl | 12 | 97 | 5322 (309) | 0.0015 (0.0015) | 1.74 | 0.200 |
| Total | | | | | | |
| Pushnet | 19 | 963 | 4959 (614) | 0.0105 (0.0156) | | |
| Midwater trawl | 18 | 890 | 5289 (340) | 0.0096 (0.0131) | 0.03 | 0.858 |

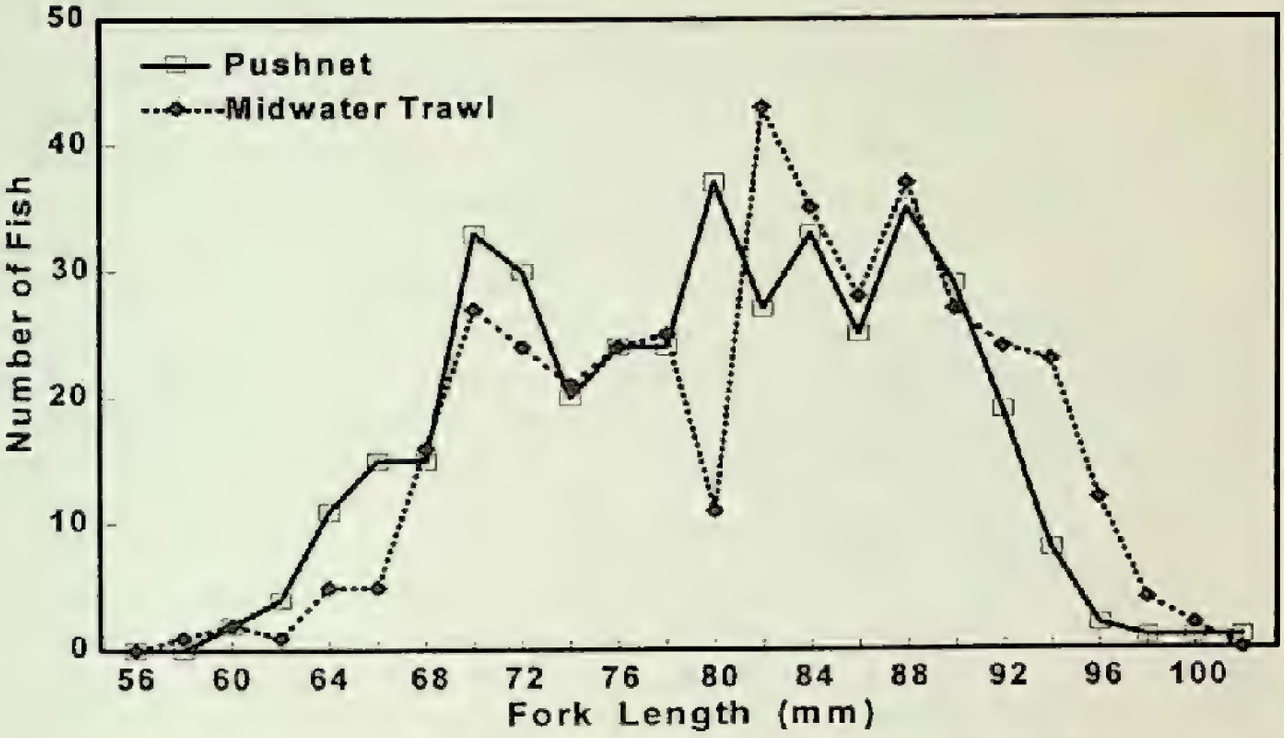


Figure 3. Length-frequency distribution of chinook salmon caught in a pushnet and midwater trawl in the Sacramento River near Courtland, California, May 1990.

Table 2. Size of chinook salmon collected in pushnet and midwater trawl in the Sacramento River near Courtland, California, May 1990.

| Date/gear | Sample size | Mean fork length (mm) | Standard deviation | Range | F | P |
|---|---|---|---|---|---|---|
| May 10 | | | | | | |
| Pushnet | 345 | 79.06 | 8.84 | 59-102 | | |
| Midwater trawl | 300 | 82.06 | 9.11 | 57-99 | 1.27 | 0.283 |
| May 25 | | | | | | |
| Pushnet | 51 | 79.49 | 6.39 | 69-95 | | |
| Midwater trawl | 97 | 79.08 | 7.06 | 67-99 | 0.08 | 0.785 |
| Total | | | | | | |
| Pushnet | 396 | 79.12 | 8.56 | 59-102 | | |
| Midwater trawl | 397 | 81.33 | 8.54 | 57-99 | 0.86 | 0.36 |

capturing juvenile chinook salmon was scheduled to coincide with the passage of about 6 million unmarked hatchery juvenile chinook salmon. The fish were released at Princeton, approximately 205 km upstream of Courtland, from 4 to 12 May 1990. The difference in fish density between the two sampling dates may be explained by a pulse of hatchery fish passing Courtland on 10 May; most hatchery fish had passed the sampling site by 25 May.

For the conditions that existed in the Sacramento River at the time I sampled, and for the size distribution of fish there, the pushnet and midwater trawl were equally

effective at capturing juvenile chinook salmon. As the pushnet samples in front of the boat, and the midwater trawl samples in the skiff's wake, disturbance caused by the boat apparently has little effect on chinook salmon catches by the midwater trawl.

If additional comparative testing in different environments corroborates the efficiency of the pushnet, it has several advantages over trawl gear: (i) It can be fished in shallower water (1.2 m) that the midwater trawl (4.6 m) because of fishing space needed by the trawl's wings and doors. (ii) Sampling effort of the pushnet is more exactly known than for the trawl because the pushnet mouth opening is fixed while the midwater trawl's mouth opening varies as wind and currents change. (iii) A pushnet can be fished in more confined areas than a midwater trawl because of its shorter length and greater maneuverability. Finally, (iv) a pushnet is cost effective, requiring a two-person crew and about 30 s to set or retrieve the net compared to a three-person crew and set and retrieval times of several minutes for a midwater trawl.

Although my study was limited to juvenile chinook salmon during a narrow range of environmental conditions, it indicates that the pushnet can be an effective sampling tool. However, to confidently use pushnets in large-scale sampling programs, additional comparative sampling in a variety of conditions and for several species is needed.

## ACKNOWLEDGMENTS

I thank R. Kano, D. Hood, J. Bull, and C. Holst for assistance in collecting data and B. Collins and D. Odenweller for providing editorial assistance. Funding for this study was provided by the California Department of Water Resources as part of the Interagency Ecological Study Program for the Sacramento-San Joaquin Estuary.

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Received: 1 May 1995
Accepted: 14 February 1996

OSP 96 77618

*California Fish and Game* 82(1):59-60 1996

# OBSERVATIONS ON USE OF TWO NON-NATIVE PLANTS BY THE POINT ARENA MOUNTAIN BEAVER

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The Point Arena mountain beaver, *Aplodontia rufa nigra*, was listed as federally endangered by the U. S. Fish and Wildlife Service (USFWS) on 12 December 1991. The limited and fragmented distribution of the subspecies, combined with threats to its habitat from various construction activities, made the listing necessary. An approved proposal by MCI Telecommunications Corporation to erect a microwave tower in habitat occupied by the mountain beaver adjacent to Manchester Beach State Park, Mendocino County, California prompted the USFWS to mandate that MCI have a biologist on site during the construction of the tower and fund a 5-yr monitoring study to determine if the project adversely affected the subspecies. It was during this study that the utilization of exotic plants by the mountain beaver was noted.

At the tower site, active mountain beaver burrows were concentrated in patches of non-native ice plant, *Carpobrotus edulis*, relative to the surrounding native vegetation. In one patch, high concentrations have continued since May 1992. This patch measured approximately 30 x 15 m, was at the base of a dune predominately covered with native vegetation, and was protected from wind by the dune.

Many mountain beaver burrows contained pieces of partially eaten ice plants. These plants apparently provided the mountain beaver with a year-round food source high in water content. The mountain beaver has primitive kidneys and limited ability to concentrate urine; it must drink daily or consume succulent vegetation (Nungesser and Pfeiffer 1965, Schmidt-Nielsen and Pfeiffer 1970). These researchers found that a captive mountain beaver survived 2.5 months on lush vegetation with no drinking water. In much of the Point Arena mountain beaver habitat, standing water is not available for most of the year. In the area containing the ice plant patch there is no available free water except for ephemeral puddles that form during rainstorms.

The mountain beaver is associated with soft soils that permit efficient burrowing. These soils enhance water drainage, which has been cited as an important factor in mountain beaver habitat (Hacker and Coblentz 1993). The ice plant formed a thick mat of vegetation that provided a firm substrate through which the mountain beaver burrowed. The root structure may stabilize the sandy soil.

Abundant vegetation is a preferred, if not essential, feature of mountain beaver habitat, which has been described as a "dense tangle of ferns, thimbleberry, and other low plants" (Camp 1918) and "coverage of a dense understory " (Zeiner et al. 1990). Some populations of the Point Arena mountain beaver occupy coastal strand and coastal scrub communities in Mendocino County. These communities often lack the

dense vegetation that provides an abundant and accessible food source, as well as protection from predation. In several areas that contain components of the coastal strand and coastal scrub communities, the Point Arena mountain beaver is associated with European beach grass, *Anmophila arenaria*, another non-native plant. Burrows are often located directly under the plants and runways travel under large mounds of dead beach grass. The plants' extensive root systems help to stabilize the sandy soils and the large canopy provides cover. However, I have not noted any evidence that the mountain beaver consumes European beach grass.

The Point Arena mountain beaver is a federally endangered species with no recovery plan and much of its fragmented population occurs in Manchester Beach State Park. Ice plant and European beach grass are two exotic plants generally deemed undesirable by resource managers; however, careful consideration should be given to the management of these exotics in Manchester Beach State Park. The importance of these plants to the animal is not fully known and further studies need to be undertaken to reveal their significance.

## ACKNOWLEDGMENTS

P.T. Northern edited and improved this manuscript. I thank him and T. Wooster for their interest in my research.

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Received: 28 March 1994
Accepted: 12 September 1994

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